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THE ORIGIN AND RELATIONSHIPS OF THE ARAUCARIANS. II

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The abietinean theory

This theory has developed more or less gradually and can best be understood by tracing the historical sequence of discovery and the ideas of relationship that have grown out of them.

1. Foremost in time and importance was the discovery that the steles of ferns, gymnosperms, and angiosperms are characterized by a leaf gap opposite the departing leaf trace. To this group was given the name Pteropsida. To the remaining groups of vascular plants the name Lycopsida was applied. This conception grew out of the investigations of the anatomy of *Equisetum* (**27**), the stem of angiosperms (**28**), and the structure and development of the stem in pteridophytes and gymnosperms (**29**). This distinction between these two great groups has been widely accepted by botanists and has formed one of the most fundamental objections in the minds of many (**16, 53**) to the lycopod theory. It has been questioned by the adherents of the latter theory (**54, 61**), but only in so far as to deny that a phyllosiphonic siphonostele (Araucarineae and possibly other conifers) might have arisen from a lycopod ancestry. The contention is that this type of stele is merely one of the important milestones along the evolutionary highway along which all vascular plants tend to travel. It is conceived to be in the same category as the heterosporic habit, the seed habit, and the tendency to reduce the size of the gametophytes.

It still remains true, notwithstanding that no known lycopod did actually cross the line.

2. Two years later (1904) came the statement of certain canons of evidence, some of which were well known and had already been employed by zoologists and to a certain extent by botanists. These are stated by JEFFREY (**31**) as follows: (1) ancestral characters that have disappeared from the vegetative axes are apt to linger in (*a*) reproductive axes, (*b*) foliar organs, (*c*) seedlings (ontogenetic recapitulation of the zoologists), (*d*) first annual ring of vigorous shoots; (2) ancestral characters may be recalled by wounding.

These canons of evidence have been consistently applied and somewhat extended in all of the subsequent work. They have been used to check conclusions derived from comparative anatomy (resemblance) and geological sequence, and in some cases practically overrule them. A really astonishing number of forms, both fossil and living, has been studied by JEFFREY and his associates in the last dozen years. Although not always without serious protest, they have been able to interpret all these forms in conformity with the general assumption that the Araucarineae have been derived from an abietineous ancestry. Much of the most important material has come from the Mesozoic of eastern North America.

A complete review of all this work is neither necessary nor profitable. Essentially the same methods have been employed in all of it. Reference will be made only to those papers in which important new facts or an advance of ideas are contained.

3. It must always be borne in mind that this school of anatomists is firmly committed to the brachyblast theory of the pine cone (**19, 42, 58**). From the vantage point of this conviction they extend the conception to the ovulate cones of all other conifers, and regard the spur shoot of the pines as the homologue of the assumed axillary sporangium-bearing shoot of the cones. The contention is that the spur shoot has disappeared from most modern conifers, as represented in its most primitive form in such ancient conifers as *Prepinus* and *Woodworthia*.

4. An additional canon was provided (1910) by Miss GERRY'S study of the distribution of the bars of Sanio in living conifers (**20**). She concluded that this structure is present in the mature secondary

wood of all conifers except the Araucarineae. It has since been used by this school as the *sine qua non* in distinguishing fossil araucarian woods from those of abietinean affinities (**9, 24, 25, 57**).

An early application (1906) of these principles was made by JEFFREY and HOLLICK (**32**). Certain of the remains studied consisted of cone scales that had previously been referred to plants of such diverse relationships as *Dammara*, fossil genera belonging to Cupressineae and Taxodineae, and even to *Eucalyptus*. These scales have three basally attached and inverted seeds on their adaxial surface. There are longitudinal resinous lines on their surface. The internal structure, particularly the arrangement of the vascular supply, is very like that of *Agathis*. For these reasons they have called the plant *Protodammara*.

Closely associated with the scales were branches of *Brachyphyllum*. The authors think it probable that the branches and cone scales belong to the same plant. The branches were sectioned and referred to the Araucarineae on the ground that of the three groups (Cupressineae, Sequoiineae, and Araucarineae) which they externally resemble, only the last agrees with them in the possession of a double leaf trace, insoluble resins accompanied by mucilage, and flattened bordered pits which may rarely be alternate and biseriate. Moreover, these branches lack the alternating bands of hard bast in the phloem characteristic of all the living members of the first two groups.

The wood fragments were of two kinds. One of them agrees with the *Brachyphyllum* branches in lacking resinous tracheids and in forming traumatic resin canals. This wood is believed by the authors to be the wood of *Brachyphyllum*. The other wood has resin tracheids and does not form traumatic resin canals. The inference from these facts is that araucarians, as represented by *Brachyphyllum*, have come from ancestors with resin canals.

In the same year (1906) JEFFREY and CHRYSLER (**33**) described certain cretaceous Pityoxyla from the same source as the *Brachyphyllum*. These Pityoxyla appear very probably to be the wood of cretaceous pines, since they are very closely associated with typical cone scales and leaf fascicles of this genus. These pines appear to have combined the characters of hard and soft pines.

The scales and leaves resemble those of the hard pines, while the presence of abundant tangential pitting of the autumn wood is a character of soft pines. The ray cells are highly resinous, and there are no ray tracheids such as are characteristic of the Pineae. The authors point out that these are just the characters shown by the wood of the cones of hard pines. They enforce their argument from vestigial structures in the following words: "there can be little doubt that in the wood of the cones of *Pinus palustris*, for example, the general absence of marginal tracheids, the highly resinous character of the rays, and the abundant presence of tangential autumnal pits, all features of difference from the vegetative wood structure of existing hard pines, are ancestral characters, since such characters are apt to linger on in the reproductive axes. In no other way can the presence of these features in the wood of the cone be explained." They call attention to the great geological age of the pines as further support of the application of these principles. "There is good reason to believe from recent researches (**33**) that the genus *Pinus* in essentially its modern form, so far as the external features of the female cones go, existed as far back as the Jurassic. There is even evidence that the two great series of the hard and soft pines existed at this early period, so that the geological extension of the genus must have been much more remote."

Following up the same line of reasoning, JEFFREY (**34**), in a paper on wound reactions of *Brachyphyllum*, put forward the suggestion that "there is nothing inherently improbable in the derivation of the Araucarineae from an abietineous stock." He puts forward three sorts of evidence in support of this suggestion.

In the first place, he points out, the wound reactions of *Brachyphyllum* are of exactly the same character as those of *Sequoia*. In a previous investigation he was led to conclude, from the traumatic production of resin canals, taken in conjunction with their vestigial occurrence in the cone axis, first annual ring of the stem, and in the root, that resin canals were characteristic of the ancestors of *Sequoia* (**30**) as well as of *Abies* and certain other Abietineae (**31**). By combining the vestigial structures exhibited by the cones of the living araucarians with the wound reactions of *Brachyphyllum*, he is led to infer a similar ancestry for Araucarineae.

The second proof brought forward in support of this conclusion is that the triassic *Araucarites moniliforme* (**34**) is reported to have strings of flattened moniliform masses of resin in the wood. The author thinks that such masses of resin would be produced by resin canals larger than those of *Brachyphyllum*. Apparently there is a reduction series in resin production in the Araucarineae. It is abundantly secreted in the canals of the triassic *Araucarites*, less abundantly in those of the cretaceous *Brachyphyllum* and only when wounded, and resin canals are entirely absent in living genera.

As a third proof a still stronger claim is made again for the antiquity of the pines. The author points to the recognized impressions of pine leaves from the Permian onward, of hard and soft pines after the Jurassic, and of Pityoxyla from the Carboniferous and Permian. It should be recalled that both the Permian and Carboniferous Pityoxyla have since been rendered extremely doubtful by the work of GOTHAN (**21, 22**) and of THOMSON and ALLIN (**71**), though undoubted Pityoxyla are known from the late Jurassic onward.

Araucariopitys was described (**35**) in 1907. The description is based on certain leafless twigs with spirally arranged scars. They were found in the Androvette pit (Cretaceous) in association with "impressions of the deciduous leaf fascicles of *Czekanowskia*, a supposed but doubtful representative of the Ginkgoales." It is inferred, with some hesitation, that the two belong to the same plant. It is shown that *Araucariopitys* had deciduous spur shoots lasting, very probably, only a single year. Traumatic resin canals were produced; the ray cells are pitted on sides and ends; the pits are usually uniseriate, round, and remote, but may occasionally be biseriate and alternate or opposite, in which case they are sometimes flattened. The uniseriate pits are also sometimes flattened and in contact. It is rather difficult to credit close araucarian affinities to this plant when one considers that it resembles a *Ginkgo* externally and has the spur shoot and pitted rays of the pines, as opposed to the slight resemblance to araucarians in the occasional occurrence of alternate and flattened pits. The authors, however, decide in favor of its being an araucarian on the ground of its close association with other araucarian woods and transitional

cone scales. If this plant really is, as the authors think, an abietinean in process of transformation, it would appear to be a question whether it were headed toward *Ginkgo*, which it resembles in external features, or toward an araucarian, which it does not resemble externally and toward which it has made but a very small beginning structurally.

In 1908 *Prepinus* was described (**37**). The name was proposed "for this type in the belief that it is the direct ancestor of *Pinus*." "It is characterized by the possession of short shoots or brachyblasts of a generalized type, which were deciduous, but bore numerous spirally arranged instead of few verticillate fascicular leaves." "The leaves attached to the brachyblasts differed from the fascicular leaves of *Pinus* in having their paired resin canals continuous to the very base. The leaves further possessed well marked centripetal xylem. About the foliar bundles was present a complicated double sheath of transfusion tissue closely related to the centrifugal wood and resembling that found in certain of the Cordaitales." "Many of the true pines of the Cretaceous possessed the same double transfusion sheath as is found in *Prepinus*, but entirely lacked the centripetal wood which is characteristic of that genus." "The elongated pitted elements described by WORSDELL and others on the ventral side of the protoxylem in existing coniferous leaves appear rather to be the relics of the inner transfusion sheath, which is a feature of cretaceous pines, than of true centripetal xylem."

From the resemblance of the leaf structure to certain Cordaitales, the conclusion is reached that the Abietineae are "a very old, if not the oldest, family of the Coniferales." From this argument, and others already detailed, it is concluded that "the Abietineae must be considered more primitive than the Araucarineae." What at first sight appears to be a new argument in support of this contention is introduced in this paper. "The pitting of the older Araucarineae, which still survived in the Middle Cretaceous, showed a marked deviation from that found in *Agathis* and *Araucaria*, and a transition toward the type of pitting found in the Abietineae, while the oldest structurally known type of the Abietineae (*Prepinus*) shows no tendency whatever toward the araucarian type of bordered pits." There is, however, nothing new in this statement,

for its entire force depends upon whether these intermediate forms are called araucarians or not. It is, of course, precisely the point at issue whether these intermediate forms are of araucarian descent on the way toward becoming Abietineae or the reverse. In fact, if this statement could be substantiated, it would completely overthrow the abietinean theory of the descent of araucarians, for this theory demands that Abietineans shall have departed in many characters, not only toward araucarians, but that this departure shall have continued until the latter were actually reached.

In 1909 SINNOTT (**57**) described from Second Cliff, Massachusetts, another fossil conifer, which he referred to a new genus, *Paracedroxylon*. The pits are uniseriate, remote, and round. The rays are without marginal tracheids, and the cells are thin-walled and without pits on the ends or horizontal walls. Simple pits occur on the radial walls corresponding to the half-bordered pits of the adjacent tracheids. Resin canals are normally absent, and no sure evidences were found of their traumatic production. The new genus, nevertheless, is assigned to the Araucarineae on the ground that bars of Sanio are absent. As I shall point out later, other anatomists have strongly objected to the reference of fossil woods to the Araucarineae on this ground.

In 1911 JEFFREY described the structure of the cone of *Geinitzia gracillima* (**41**) from the Kreischerville beds. This piece of investigation furnishes a very interesting application of the canons of evidence that have been applied in the attempt to seriate these fossil types, for it furnishes an attempt to make a comparative study of the structures of the vegetative and reproductive axes of the same fossil plant, and to apply to the results the canon of vestigial structures. The external appearance of the cones, as well as the individual scales, are very reminiscent of certain Taxodineae. The branches are thought to be *Brachyphyllum*. The structure of the cone axis is that of SINNOTT's *Paracedroxylon* (**57**). From these facts the conclusions follow that *Paracedroxylon* is ancestral to *Brachyoxylon;* that the evolutionary sequence must have been Abietineae (*Pityoxylon*, perhaps), *Paracedroxylon*, *Brachyoxylon*, *Araucarioxylon*, modern Araucarineae. It will be pointed out

later that this scarcely accords with the strict geological sequence as known at the present writing.

Woodworthia arizonica was described in 1910 by JEFFREY as a new genus from the triassic petrified forests of Arizona (**38**). It agrees in all respects with *Araucarioxylon*, with the exception of possessing short shoots and the absence of persistent leaf traces. The spur shoots are thought to persist as long as the axis which bore them. The spur shoots are held to show a relationship to the pine type of conifer. The failure of the subtending leaf traces to persist indefinitely, as in living forms, is held to be an argument against this persistence being a primitive character. Notwithstanding the fact that the cretaceous *Araucariopitys* is much more abietinean in all respects and a much more modern type, the author is still disposed to cite the two as evidence of "the tendency of the Araucarineae to become more and more like the Abietineae."

In 1911 BAILEY described a cretaceous *Pityoxylon* with marginal tracheids and concluded (**2**) that such marginal tracheids originated in the Upper Cretaceous. In a paper published in 1913, Miss HOLDEN has extended our knowledge of the generic and geologic distribution of ray tracheids (**25**). She concludes from her study that (1) "ray tracheids are present normally in the Pityoxyla from the Middle Cretaceous on, and in the Abietineae"; (2) "ray tracheids are present traumatically in the Taxodineae and the Cupressineae"; (3) "on the evidence of traumatic recapitulations of ancestral characteristics, it is evident that the Taxodineae and Cupressineae are descended from the Abietineae, having sprung from that line sometime after the Middle Cretaceous"; (4) "since ray tracheids are universally absent in the Podocarpineae, Taxineae, and Araucarineae, these lines must have come off the Abietineae at some time before the Middle Cretaceous."

In 1912 JEFFREY published a very complete résumé (**42**) of his views and investigations. The first part of the paper deals with wood parenchyma and medullary rays. He concludes: (1) "The ancestors of *Araucaria* and *Agathis* were characterized by the possession of wood parenchyma." This conclusion rests on the facts that, though the living forms resemble the Cordaitales in the absence of wood parenchyma, it is present in the first annual rings of

the root and shoot of both *Agathis* and *Araucaria*, in the early wood of seedlings, in the wood of the cones, and may be traumatically recalled in the older wood of both root and shoot. Furthermore, it is present in the more abietinean Araucarioxyla of the Cretaceous. (2) "They likewise had strongly pitted rays." This is shown by their presence in the inner portion of the cone axis of living forms and in the normal wood of those cretaceous forms (*Araucariopitys*, for example) which the author assigns to the Araucarineae. Pitted rays may also be recalled in the seedling and root by injury. (3) "The possession of these two features is quite inconsistent with their derivation from cordaitean ancestry," notwithstanding the practical identity of structure of the two groups. This argument rests partly on recapitulationary phenomena and partly on merely calling the transitional cretaceous conifers araucarians rather than abietineans, which some of them resemble far more closely.

The second part deals with "the characteristic features of the tracheids and the nature of the pitting." The conclusions are: (1) "The characteristic pitting of the wood of *Agathis* and *Araucaria*, the *Araucarioxylon* type, is not ancestral but more recently acquired." This conclusion is based on the fact that the multiseriate, flattened, and appressed pits of the mature wood of living araucarians and of Cordaitales is replaced in the inner wood of the cone and seedling axis of living genera and in the innermost wood of the stem of mesozoic forms by a type of pitting with the pits less frequently multiseriate, flattened, or appressed, but often uniseriate, remote, and round. (2) Since bars of Sanio are absent from the mature wood of living genera (see THOMSON **70** for a contrary opinion) and from the wood of mesozoic Araucarioxyla, but are present in the wood of the cones, it follows that they are a feature of the ancestors of the Araucarineae. In anticipation of objections to be urged later, it may be mentioned here that the author admits their absence in the stem of the mesozoic forms, in the seedling, and probably in the leaf trace, in all of which they should be found in accordance with theoretical expectations. (3) "On the basis of comparative studies of the tracheids of the Araucarineae they cannot be regarded as primitive representatives of the coniferous order."

The third part deals with resin canals. Two reasons are alleged for thinking them to be features of the ancestors of araucarians: (1) Though they are practically absent from living araucarians, "interesting vestigial resin canals appear in the vascular supply of the lowermost abortive cone scales, attached to the peduncle of the cone, and die out before the cone scale supply leaves the wood of the peduncular axis." (2) Traumatic resin canals occur in the wood of some mesozoic woods which the author assigns to the Araucarineae because of the lack of the bars of Sanio and the possession of a modified type of pitting. The pitting in the *Araucariopitys* type, as has already been pointed out, is very little like that of araucarians and very much like that of abietineans, as are, in fact, its other characters. The *Brachyoxylon* type is rather more reminiscent of araucarian affinities but still not beyond challenge.

The fourth part treats of the foliar trace and the pith, and presents a final summing up of conclusions. In regard to the leaf traces and pith the conclusions are: (1) "This persistence of the leaf trace [that is, in mesozoic forms] seems to be a characteristic of all woods of the true *Araucarioxylon* type, and, as has been particularly indicated by THISTLETON-DYER (**66**) and SEWARD (**54**), is likewise a feature of the trunks of the living genera *Agathis* and *Araucaria*." (2) In the *Brachyoxylon* type from the Cretaceous, which is more abietinean in the rays, pitting, and in the formation of traumatic resin canals, the traces persist for a short time only. (3) In the seedling axis of *Agathis australis* the leaf trace is less persistent. (4) The leaf trace is more persistent in *Araucaria Bidwillii* than in *Agathis australis*, the former of which is assumed to be the more primitive type. (5) It follows from the preceding that persistent leaf traces are not an ancestral feature of the Araucarineae. (6) In regard to the pith I am not at all sure that I apprehend clearly JEFFREY'S position. He records the usual presence of sclerotic diaphragms in the pith of mesozoic forms, and finds them absent in the pith of the seedlings and cones of living forms. Sclerotic nests are said to occur in the latter, perhaps as a vestige of the diaphragms of the earlier forms. He says further that "it is moreover obvious that medullary diaphragms are equally characteristic of both the older Araucarineae and of the Abietineae living and

fossil. Their presence in the older araucarian types, consequently, is one more piece of evidence in favor of the derivation of the araucarian tribe from abietineous ancestors." (7) The author reiterates his belief in the compound nature of the ovulate cone and in its essential unity throughout the group. He says, "it is perfectly clear that not only in the more primitive species of the living genus *Araucaria*, but also in the cones of the mesozoic representatives, the araucarian female cone, like that of the other tribes of conifers, was originally composed of cone scales with a double system of bundles, independently emanating from the cone axis and of inverse orientation." (8) In regard to the male gametophyte he says, "certainly we should not expect to find the primitive type of pollen tube formation in a group in which the pollen no longer reaches the apex of the ovule," and "the peculiar method of germination of the pollen is an unmistakable stigma of aberration." "The contents of the pollen tube likewise vouch for the highly specialized condition of the Araucarineae. Here the two prothallial cells common to the Abietineae and the equally ancient Ginkgoales become proliferated into a large number, doubtless in correlation with the extreme length and meandering course of the pollen tube. Moreover, the absence of a stalk cell in connection with the setting off of the body cell, which gives rise to the two sperm cells, is a clear and outstanding feature of aberrancy." These views are in a measure a modified restatement of those stated by JEFFREY and CHRYSLER in 1907 (**36**). JEFFREY is equally convinced that the female gametophyte is not primitive but aberrant.

In a very complete study of *Agathis* (**19**) EAMES has reached conclusions closely paralleling those of JEFFREY in regard to the specialization of the gametophytes and the interpretation of the structure of the ovulate cone of the araucarians. An interesting and important feature of this investigation is the very complete reduction series which he has worked out in the supposed development of the apparently simple scales of *Agathis*. Beginning with *Arthrotaxis cupressoides* with a completely double vascular supply, he traces the gradual fusion of the independent bundles through other species of the same genus, *Cunninghamia sinensis*, and finally reaches the condition found in *Agathis*. He also points out

that a complete series is exhibited in the genus *Araucaria* with *A. Bidwillii* standing as the most primitive and *A. brasiliensis* and *A. imbricata* as the most specialized. In preceding papers of this series the reviewer has discussed EAMES's views in relation to the gametophytes (**6**) and the embryo (**7**).

Although SINNOTT (**59**) concludes from his study of the podocarps that they have been derived from the Abietineae directly, and not through the Araucarineae, his view is incidentally interesting in that it points out that on this assumption the podocarps become the primitive members of the group instead of the *Saxegothaea-Microcachrys* forms. In his diagram it would appear that he thinks this whole assemblage derived from the ancient Araucarineae, and that they had arisen by an approximately equal split of some ancient Abietineae, the other arm being the modern abietineans. From the text, however, it appears that "the close series of forms from *Podocarpus* to *Saxegothaea* is very suggestive as offering a key to the evolutionary development of the modern Araucarineae." The argument turns on the interpretation of the vascular supply in these forms as a reduction series and the epimatium as the equivalent of a reduced ovuliferous scale. He calls attention to the already well known gametophytic resemblances, which his own studies have rendered more apparent, as evidence of a relationship between podocarps and Abietineae. In like manner he minimizes the points of difference. He recognizes that his series can be read in the other direction, and calls attention to the necessity in that case of recognizing and accounting for what would be numerous parallel developments in the two lines.

In the concluding section of his paper on the *Araucarioxylon* type (**42**) JEFFREY sums up the conclusions for the whole theory as follows: (1) "The Araucarineae cannot have been derived from the Cordaitales since they possessed primitively a number of features which, so far as our knowledge goes, never existed in the cordaitean stock." (2) "The *Araucarioxylon* type is derived from ancestral forms which possessed opposite pitting, bars of Sanio, strongly pitted rays, and horizontal and vertical resin canals." (3) "The primitive existence of these features in the ancestral type from which *Araucarioxylon* has been derived shows clearly that it has taken its

origin from the abietineous *Pityoxylon* type." (4) "This conclusion is entirely confirmed by a consideration of the reproductive structures, both sporophytic and gametophytic." (5) "Any hypothesis as to the origin of the Coniferales in general must start with the Abietineae as the most primitive tribe."

This theory has received from time to time certain incidental criticism in connection with the work of investigators who have considered that their results justify other interpretations. A number of these have already been mentioned in the presentation of the lycopod and cordaitean theory. It is in the nature of things that the facts which form the support of one theory are usually the facts that refuse to adjust themselves easily to others. Objections of this sort have found their proper place in the preceding paragraphs. I shall now mention some of the more specific objections that have been made.

It has already been pointed out that the protagonists of the lycopod theory hold the ovulate cone of the araucarians to be simple. The abietinean theory is circumscribed by the necessity of proving it compound. The weight of opinion, at least so far as numbers go, among those who have investigated the subject appears very decidedly to favor the idea that the ovulate structures of podocarps and araucarians are homologous in structure and simple. It appears from the work of EAMES and SINNOTT, already quoted above, that if the abietinean theory prevails they can be explained as a reduction series. On the other hand, if this theory were not in question, it appears that most investigators would decide in favor of simplicity of structure. Aside from the authors already mentioned, TISON (**76**) and NOREN (**44**) have expressed themselves in favor of a simple explanation.

The writer has in earlier papers called attention to the inadequacy of the explanation offered by JEFFREY and CHRYSLER (**36**) of the more numerous prothallial cells in the gametophytes of podocarps and araucarians. These authors suggested that the greater number of these cells might be a coenogenetic adaptation to the extensive pollen tube. Aside from the reasons for thinking that the tube itself has not undergone any such coenogenetic development as this theory suggests (by implication) for the araucarians, it is

entirely inapplicable to the podocarps and *Abies* (**26**), which has recently been shown to form regularly a considerable proportion of pollen grains with 3 or 4 prothallial cells. Either these widely separated cases are to be explained as a heritage from more or less remote ancestors, or as remarkable examples of the revival of abandoned structures, or as the still more remarkable origination of apparently useless structures. In JEFFREY'S paper on the *Araucarioxylon* type (**42**) he speaks of the pollen grain and male gametophyte as clearly aberrant in its germination, prothallial cells, and absence of a stalk cell. Whether it is aberrant or not is doubtless somewhat a matter of opinion. That a stalk cell is not formed is an error so far as the statement concerns *Araucaria brasiliensis*. I have figured in a previous paper the division which results in stalk and body cells (**5**). *Araucaria* resembles *Podocarpus* (**4**) exactly in respect to the manner of this division. The axis of the spindle is transverse in both cases and the resulting cells lie side by side above the prothallial cells. Because this division occurs late in the development of the male gametophyte, the cell wall and cell identity of the stalk cell are soon lost in both genera. At the time of shedding, only the body cell retains its cell identity, the other nuclei being free in the common cytoplasm and often indistinguishable from one another.

The reference of some of the mesozoic fossils to Araucarineae has met with rather severe criticism. JEFFREY'S reference (**40**) of *Yezonia* and *Cryptomeriopsis* (**62**) to *Brachyphyllum* and *Geinitzia* respectively has met with opposition from their authors (**63**). Dr. STOPES, notwithstanding the dissimilarity of the cones, is inclined to agree that there is a considerable structural resemblance between *Brachyphyllum* and *Yezonia*. She dissents entirely from the opinion that *Cryptomeriopsis* is an araucarian. She has not stated an opinion as to whether it is or is not identical with *Geinitzia* as described by JEFFREY (**41**). She is emphatic, however, in thinking that it differs very little from the modern *Cryptomeria*.

STILES (**61**) has also criticized the reference of *Geinitzia* (**41**) and *Paracedroxylon* (**57**) to the Araucarineae. He is particularly severe on the use of the bars of Sanio as a final criterion of relationship. The soundness of this criticism has since been emphasized by

THOMSON's discovery of these bars of Sanio in the ordinary wood of araucarians (**70**). They have also recently been reported in the cycads (**56**). In this group they are said to occur when the pits are scattered, but not when alternate and crowded.

THOMSON (**70**) has suggested that the araucarian affinities of some of the mesozoic transitional forms with traumatic resin canals would be equally well explained as having descended from the cordaiteans as by the assumption that they are acquiring araucarian characters. If I understand this suggestion correctly, it assumes that these forms are not directly related to araucarians at all, but are really abietineans that still retain some cordaitean characters and have acquired or are in the process of acquiring the characters of modern abietineans.

On the principles of evidence

After having set forth the evidence that has been adduced by various writers in support of the several theories, it is now pertinent to return to the problem originally proposed by the quotation from JEFFREY. Are there any general principles of evidence or are there not? Are all sorts of evidence of equal value? Shall any class of evidence be excluded, as is done in our law courts? Such questions as these must be answered by every botanist before he can properly proceed to sound inferences from the facts uncovered by his investigation. The arguments set forth in the preceding sections may be conveniently grouped under the following heads: (1) resemblance or likeness, (2) geological sequence, (3) vestigial structures, (4) ontogenetic recapitulations, (5) traumatic reversions, (6) abnormalities or monstrosities.

1. *Resemblance or likeness means relationship.*—This appears to be the most fundamental principle in the minds of the great majority of writers on this and other phylogenetic problems. That this is a sound principle is unquestioned. No fact in our biological experience is better grounded than that "like begets like." That the parent and child may differ in minor points is an everyday experience, but that they ever differ by large differences is not believed. The theory of evolution itself is founded firmly on these two well known facts of general likeness with slight variations.

From this it follows that affinity is roughly proportional to resemblance. Resemblance in one or a few points may mean a slight degree of affinity, or it may merely show a case of parallel development. Heterospory and the seed habit are excellent illustrations of the latter. If, on the contrary, two plants are very similar in all of their organs, the resemblance is usually considered unimpeachable evidence of close affinity. The classification of all our living plants is almost exclusively based on this principle.

A corollary of this principle is that neither of two supposedly related plants must possess any organ or structure which cannot be reasonably derived from the homologous organ or structure of the assumed ancestor.

2. *The geological sequence* should roughly conform to the proposed evolutionary sequence in the development of a modern group from an ancient one. It is obvious that if all the intermediate forms have been fossilized and all discovered, this agreement would be exact and complete. Such conditions doubtless never occur. Since evolution of related forms cannot be supposed to run exactly parallel in different lines, it follows that the discovered fossils from any given horizon might be expected to show one structure or organ ahead in one and another in another. An important corollary of this has frequently been insisted on by COULTER (**14, 15, 16**). One line of plants may run ahead along a certain line and remain practically stationary for ages in some other. For these reasons and because the fossil record is always very incomplete, inferences from geological sequence must always be subject to considerable doubt.

3. *Vestigial structures.*—By this is meant that anatomical characters that once were general through the entire plant are likely to be retained in certain supposedly primitive regions of the plant, such as the root, cotyledons, cone axes, and leaves. The use of this principle is attended with very considerable difficulties and may frequently lead to very erroneous conclusions. The difficulties lie in two assumptions that must be made in its application. First, we must assume that the stem structure of a paleozoic (let us say) plant was also present in the cone axis. Then when we find this same structure in the cone axis of a modern plant, we must again assume

that this structure is a retained one and not a newly acquired one. If we could avoid the first assumption (that is, if we knew the structure of the ancient cone), we should not need this principle, but could apply the principle of resemblance. Neither is it always easy to decide the correctness of the second assumption. Its limitations, therefore, are clear. It is useful in enabling us to infer a likeness which we do not know actually to have existed. It is, consequently, of much lower value than a direct comparison of known structures. Its highest possible value would equal that of a direct comparison between the homologous parts of the two plants, while its lowest value is actually zero.

4. *Ontogenetic recapitulations.*—This principle assumes that there will be formed in the juvenile stages of a plant or animal organs or structures that were characteristic of the adult ancestral forms. In the form I have stated it, this principle is almost certainly invalid. This is the form in which it is commonly applied. What is probably true is that related animals and plants resemble one another and their common ancestor at all stages from the egg to the adult, inclusive, in all those organs and structures which have neither been lost since the separation from the parent stock nor added to either of the descendants. This principle is not infrequently applied in such a manner as to deprive the conclusions of any real validity whatever. In so far as it possesses validity at all, it owes it to a direct comparison of homologous structures in the same stage of development.

5. *Traumatic reactions.*—When a plant or animal is wounded it not infrequently reacts by forming organs or structures that differ from those usually formed. In some cases these structures are such as are thought to be identical with those of its ancestors. There is no a priori reason why they should be reversions, so far as I can see, unless the original structures were introduced into the sum of the hereditary qualities through wounding in the first place. Pruning a grape vine or a fruit tree usually induces a yield of larger fruit or even a greater total quantity. Increased physiological activity is a very common result of wounding, but it does not therefore follow that this is an ancestral quality of the stock. Some of these responses may represent ancestral conditions, but it seems to

me to be very unsafe to infer that any particular one is so, without independent proof thereof.

6. *Monstrosities or abnormalities.*—So far as concerns inherited abnormalities, it must be true that in the long run the progressive changes must have much exceeded the reversions, else evolution from the simpler ancestors to the more complex descendants of today could not have occurred. This argument cannot be applied in the same way to non-heritable abnormalities, though there is no obvious reason why they should follow any different law of probability. By themselves, abnormalities afford evidence of little weight, since it is impossible to say whether they represent reversions or other chance variations.

Conclusions

We may now attempt to apply these criteria of evidence to the arguments that have been offered by the various supporters of each of the theories. So far as concerns the lycopod theory and the cordaitean theory, it is readily seen that each of them is founded on certain more or less striking resemblances. The evidence, then, is valid so far as the principles are concerned. The weakness of each theory lies in the necessity of certain more or less plausible explanations that must be accepted before the resemblances are evident. The lycopod theory must explain away the very apparent difference in the stelar structures of the two groups and must show how the pine cone has been evolved from the simple cone of a club moss. Without repeating what has already been set forth in other parts of this paper, let it suffice to recall the very large number of points of difference that must be explained away and the comparatively few points of likeness relied on to establish a relationship.

On the contrary, the points of resemblance between araucarians and Cordaitales are numerous and striking. The points of difference are few, and for the most part more easily explained away than those that confront the preceding theory. The geological record appears also to favor the cordaitean theory, for none of the fossil forms are known to approach lycopods in any character more closely than do the modern forms. In fact, it would appear from our present knowledge that the fossil forms were less like them than the

modern ones. This would strongly indicate parallel development of similar structures in the two groups. On the evidence, then, as it stands, we must decide that the cordaitean theory is much the more probable.

In respect to the abietinean theory we meet a different state of affairs. It is not claimed that Abietineae are more like cordaiteans than araucarians, but that it can be shown that the likenesses of the latter have been secondarily acquired. This is not parallel development. The theory assumes that a considerable number of characters underwent extensive modification during the evolution of the primitive conifers (that is, abietineans). Multiseriate bordered pits of the cordaiteans became uniseriate, remote, and rounded. The thin-walled unpitted ray cells became thick-walled and pitted. Resin canals were evolved. Then this primitive stock is conceived to have split into two lines, one of which continued its evolution along the same lines as the parent stock. The other line (araucarians) faced about and began the reacquisition of the characters that had been lost. It almost completely regained the original type of pitting, lost all trace of its pitted rays, and almost totally lost the ability to produce resin canals in the wood. The history of other characters is much the same. The adherents of this theory do not seek to deny these resemblances nor the necessity of showing that they have been secondarily acquired. I have already set forth the evidence through which they believe that they have proved this astounding evolutionary sequence. So far as resemblance or likeness goes, the cordaitean theory is far and away the more probable.

On the basis of fossil history there is not much to choose in respect to antiquity of the two families, though the Araucarineae have, perhaps, at present the more certain record in the older rocks. Still, specialized abietineans are known so far back that we must assume their origin to have been very much farther back. I shall speak of the bearing of the transitional fossils of the Mesozoic after discussing the remaining canons of evidence, because it is only in the light of the inferences made in accord with them that these fossils can be made to support this theory. On the basis of geological sequence they favor the cordaitean theory, inasmuch

as the older forms are more araucarian and the more recent ones more like modern Pinaceae, particularly certain Taxodineae and Sequoiineae.

Though the argument from resemblance and geological sequence is unfavorable to this theory, there are, nevertheless, a great many known facts that can be best explained in accordance with it. The evidence derived from a study of vestigial structures, recapitulations, traumatic reversions, and monstrosities largely favors this theory, though many facts are known which appear to be inconsistent with it.

The pitting of the tracheids in the ovulate cones has been interpreted by THOMSON and JEFFREY in exactly opposite ways. The former calls attention to the multiseriate (3–5 rows) cordaitean pits of the older wood, and the latter to the uniseriate wood of the first few tracheids. To make matters worse, the former calls attention to araucarian pitting in abietinean cones and roots. This could, of course, be explained as a heritage from the cordaiteans.

The argument from recapitulation is hardly more fortunate. The seedling pine lacks spur shoots, just as does *Araucaria*, and hence spur shoots are not ancestral; but on the other hand the seedling *Araucaria* has abietinean pitting in the earlier annual rings.

Similarly, wounding an araucarian produces no resin canals, though it should if this theory be true; though wounding *Brachyphyllum* did. In other cases it does recall or induce abietinean characters.

The use that has been made of the bars of Sanio appears to the reviewer to fall in a class by itself. From the time of LINNAEUS' classification of flowering plants down to the present many such artificial distinctions have been proposed. They have usually been short-lived. Inasmuch as a bar of Sanio must have been at some time acquired, one would suppose that if you traced the ancestral line backward it would gradually fade out. In that case there would certainly be Abietineae somewhere along the line that lacked this structure. THOMPSON'S discovery of its presence in mature secondary wood of modern araucarians renders

its use of very doubtful value. It seems very unlikely that its mere absence from a mesozoic form otherwise unlike an araucarian is a character of sufficient importance to justify its inclusion in the Araucarineae.

The argument from abnormalities as applied to this theory is subject to attack on the historical side as well as on the ground of inherent probability. That a given abnormality represents always a reversion is an assumption that no one seriously maintains. For example, six toes are not uncommon in mankind. No one believes that this is an ancestral character any more than brachydactyly, where there are fewer parts than usual. An extra digit in hoofed animals is, on the contrary, usually looked on as a reappearance of an ancestral condition, because this condition is believed on other and trustworthy grounds actually to have occurred in this evolutionary line. In respect to the known conditions of the cones that may be supposed to be ancestral to modern pines, there is not a scintilla of evidence that they were any nearer the brachyblastic condition than their modern representatives. As I have already pointed out, the case is still more difficult in regard to the Cordaitales, the supposed remote ancestors, where the condition should, theoretically, be well developed. The strength of this theory is that it explains the pine cone, and its weakness is that it makes it necessary to apply the same explanation to other cones and shoots where it is very much less satisfying.

To sum up, the argument for the abietinean theory, therefore, is seen to be of a less convincing kind. Moreover, there are other arguments of the same kind that favor the cordaitean theory.

It seems clear to the writer, also, that there are well defined rules of evidence in the investigation of phylogenetic problems, but that the conclusions attained through their application have far less certainty than a chemical analysis or a mathematical prediction of a comet's course. With care the latter attains a high degree of certainty. The degree of probability in phylogenetic inquiries is more nearly that pertaining to the verdict of juries in our law courts. They are both always subject to attack by the introduction of new evidence.

Summary

1. The science of phylogeny possesses fairly adequate and reasonably trustworthy rules of evidence.

2. The degree of relationship is most clearly indicated by a detailed and accurate comparison of all the structures of the plant in all the stages of development, and is roughly proportional to the number and exactness of the resemblances.

3. Conclusions derived from direct comparisons should be checked carefully by the geological record.

4. Direct comparisons may be supplemented by indirect comparisons instituted through the use of more or less valid conclusions derived from the presence of supposed vestigial structures in primitive regions and from recapitulationary phenomena. Such indirect comparisons afford much less certain conclusions.

5. Reversions to ancestral conditions may sometimes occur under normal conditions or be experimentally produced by wounding or unusual conditions of growth. Conclusions based on evidence of this sort have little weight unless supported by other more reliable sorts of evidence.

6. Gymnosperms as a group resemble one another much more closely in very many ways than any one of them resembles any other group. They are, therefore, monophyletic. Since the cycadophytes are almost certainly derived from a filicinean ancestry, it follows that all are ultimately traceable to the same source.

7. The conifers closely resemble Cordaitales and are probably derived from them.

8. Araucarineae resemble the Cordaitales far more closely than do any other conifers, and are probably derived directly from them. This conclusion is consistent with the geological record.

9. The transitional conifers of the Mesozoic are either araucarians or cordaiteans well on their way toward Pinaceae. Some of them may be actually ancestral to such Taxodineae as *Cryptomeria* and *Sequoia*.

10. The Abietineae are very old and are derived either directly from the Cordaitales or from the very ancient members of the Araucarineae.

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TAXONOMY AND DISTRIBUTION OF ERIODICTYON

LeRoy Abrams and Frank J. Smiley

(WITH THREE FIGURES)

In 1905, Chancellor Jordan (**7**), in reviving the isolation theory, presented the following general law: "Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort."

Botanists were not agreed as to the applicability of the law to plants, and Lloyd (**8**) even asserted that it "would be more in harmony with the facts in the case as understood by the botanists if stated in the converse form." At the time we were inclined to accept the law and offered (**1**) a number of illustrations in support. But it was obvious that very few data on the distribution of plants in this country were available. Few attempts had been made to map accurately the distribution of closely related species. Distributional notes in the manuals were of such a general nature that they were largely useless for such a study, and many of the herbarium specimens were but little better, the average collector's data being far too meager and often confusing. The need for careful distributional studies of closely related species seemed imperative, and with this in mind we have been collecting data on a number of Pacific Coast genera.

Eriodictyon was selected as one of the genera for these distributional studies for various reasons. The species constitute a single clearly defined natural group instead of an aggregate of groups, as is often the case with the larger genera; they are all evergreen shrubs readily detected in the field at all times of the year; and, finally, their center of distribution is in southern California, the region with which we are most familiar.

As originally recognized by Bentham (**2**) and Gray (**4**) and as recently delimited by Brand (**3**), the genus *Eriodictyon* comprises a small natural group of sclerophyllous shrubs peculiar to California and the Southwest, where they are commonly called

"Yerba Santa." All the species are essentially Upper Sonoran, but range in their zonal distribution from the upper edge of the Lower Sonoran to the Transition.

Propagation may be by seed or, at least in *E. californicum*, it may be by suckers; whole colonies or thickets are often connected by lateral roots that lie only three or four inches below the surface of the ground. In the xerophytic habitat where these plants usually grow, ability to propagate in this manner is an effective factor, for seedlings have difficulty withstanding the long dry seasons.

The leaves present striking examples of adaptations to xerophytic conditions, which fall into two categories. One type, represented by *E. californicum*, has the upper surface covered by sessile glands that give a smooth varnished appearance, and the lower surface conspicuously reticulate-veined with the stomatic surface in the sunken meshes clothed more or less densely with a short grayish tomentum. The palisade tissue is also prominent, comprising several tiers of cells. Other xerophytic adaptations in this type are mainly in the reduction of leaf surface; in *E. californicum*, an inhabitant of central and northern California, the normal leaf is flat and 10–15 mm. wide, while in *E. angustifolium*, of the Arizona mountains, where xerophytic conditions are more severe, the leaves are revolute and only 2–5 mm. wide.

In the other foliage type, represented by *E. crassifolium*, both surfaces of the leaves are clothed with thick-walled unicellular trichomes that form a dense mat over the entire surfaces. In *E. tomentosum* these trichomes stand out at right angles to the surface for a short distance, then turn sharply and interlace, forming a dense felt just above the surface; by this arrangement a sort of "ramada" is produced which shuts off the sun's rays and the hot winds, but allows slow diffusion. The palisade layer is much less developed than in the glutinous type, comprising a single tier of cells instead of several tiers. The leaves are also broader and never revolute.

It is evident that the members of the genus are adapted to xerophytic conditions, and that two diverse methods of meeting these conditions have been evolved. That the two types have

sprung from a common stock is also evident, for, as we shall show, there are forms still existing that comprise an almost unbroken series from the glutinous to the tomentose type.

FIG. 1.—*Eriodictyon crassifolium* Benth.: type specimen in the Bentham Herbarium at Kew Gardens.

Since *E. crassifolium*, a typical tomentose form, inhabits the San Diego region, and *E. californicum*, a glutinous form, the more humid central and northern California, it would indicate that a direct environmental influence was the causal factor in evolving the two types. That is to say, if specimens of the two types were grown under the same environment they would eventually become alike, but that is a point that remains as an enticing future problem. From the present studies, however, we learn that other members of the glutinous series occur in the San Bernardino Valley and even in the vicinity of Ensenada, Lower California, where they are subjected to more severe xerophytic conditions than are members of the tomentose type in the Los Angeles region. These distributional facts demonstrate that the glutinous forms may be as well fitted to a xerophytic environment as those of the tomentose group. We may with equal propriety, therefore, suggest that the two groups represent two strains of a common stock that have developed independently. This theory is borne out further by the fact that forms of the two groups growing in contiguous territories more or less intergrade where they meet; while in isolated regions, where only one strain is represented, no marked variation occurs even in strikingly different environmental conditions. As an example, *E. californicum* is the only species represented on the Santa Cruz Mountain peninsula, while no related form extends north of the Santa Barbara region. On this peninsula various climatic conditions are at hand, and if the glutinous and tomentose types simply represent more or less xerophytic conditions, we should find some indications of the two strains; but such is not the case. Plants have been observed associated with the madroño, California black oak, thimbleberry, and similar plants in mesophytic conditions, where the average annual rainfall is approximately 40 inches and where the rainless summers are ameliorated by frequent coast fogs. Other plants have been observed growing in typical xerophytic chaparral, where the annual rainfall is less than half as much and summer fogs very infrequent. The only difference detected between the plants from these two stations was found in the stature of the plants and in the size of the leaves.

It is not possible in this preliminary work to prove or disprove the "Jordan law," but it is evident that the species of *Eriodictyon* conform remarkably. We wish to reiterate, however, that mere

FIG. 2.—*Eriodictyon tomentosum* Benth.: type specimen in the Bentham Herbarium at Kew Gardens.

isolation has not been the primary factor in evolving these forms. That would hardly be argued by anyone. Isolation is no more a causal factor in variation or mutation than is artificial segregation, but like artificial segregation, as practiced by all breeders and experimental evolutionists, it is of prime importance in preserving new variations or mutations. We saw at the outset that our method of investigation was not such as to divulge the real underlying factors that have brought about the different forms of *Eriodictyon*. It must be supplemented with experimental studies, but whether it is possible to conduct these experiments successfully remains a future problem. For the present it has been our aim to ascertain, first of all, what forms exist in the group selected, and so far as possible where and under what conditions they grow. With data of this nature available, the experimental work can be undertaken by anyone with a clearer conception of the problem, and with more likelihood of interpreting rightly the results of his experiments.

ERIODICTYON Benth. Bot. Voy. Sulphur 35. 1844.

Low shrubs with thin shreddy bark and persistent, alternate, toothed or rarely entire leaves, tapering at the base to a more or less evident petiole, or sessile in one species, of firm coriaceous texture. Flowers in a terminal, usually naked, panicle of scorpioid cymes. Sepals linear, not enlarged above. Corolla funnelform to nearly campanulate, pale or dark violet or white. Filaments more or less adnate to the corolla and included, usually hirsute and of irregular length. Ovary 2-celled by the meeting of the dilated placentae in the axis. Capsule first loculicidal then septicidal, thus 4-valved, each valve with a short beak and closed on one side by the adherent dissepiment or half-partition. Seeds brown or black, finely reticulate with ridges running lengthwise, and connecting them many cross-bars.

A genus of eight species restricted to southwestern United States and adjacent Mexico, where they extend from southern Oregon and southern Nevada and Utah through Arizona and California to northern Lower California, but they belong essentially to the California element, and six of the species occur within and are practically confined to that state.

In addition to the species included in these studies, there are two other plants which were transferred by GREENE (**5, 6**) from

FIG. 3.—Distributional map of *Eriodictyon:* each species is given the same number as in the text; species 1–5 are outlined by an unbroken line and the stations cited in the text are marked by a circle; species 6–8 are outlined by a dotted line and the stations by a black dot.

Nama to *Eriodictyon*. *Nama Parryi* Gray agrees with typical *Eriodictyon* in seed character and essentially in fruit, and perhaps

should be placed here rather than in *Nama*, but it is an ill-scented herbaceous perennial of a totally different habit from true *Eriodictyon* and at least worthy of subgeneric distinction. The other species, *Nama Lobbii* Gray, has seeds merely muriculately papillose without any traces of longitudinal ridges, a seed character of the *Nama* type, and it is with that genus that it is most closely related.

Leaves petioled; herbage glutinous or tomentose, not hirsute.
- Herbage not grayish or hoary tomentose throughout; upper surface of the leaves glabrous and glutinous.
  - Branches glabrous and glutinous or those of the panicle sparsely pubescent; reticulations evident on the lower surface of the leaves.
    - Corolla tube about 12 mm. long, lavender-purple, much exceeding the nearly glabrous sepals ..... 1. *E. californicum.*
    - Corolla tube 5–7 mm. long, little or not at all exceeding the sepals, white.
      - Leaves mostly broadly lanceolate, not revolute; sepals densely pubescent; filaments adnate to the corolla tube half their length ..... 2. *E. trichocalyx*
      - Leaves mostly narrowly linear and revolute; sepals usually sparsely pubescent; filaments adnate one-third their length ..... 3. *E. angustifolium.*
  - Branches tomentose, becoming more or less denuded with age in *lanatum.*
    - Leaves lanceolate, firm-coriaceous and more or less revolute, densely white-tomentose beneath, obscuring the reticulations. 4. *E. lanatum.*
    - Leaves broadly oblanceolate, not revolute; sparsely soft-tomentose beneath; reticulations evident. 5*b*. *E. c. denudatum.*
- Herbage more or less densely tomentose throughout.
  - Calyx and corolla not glandular-pubescent; corolla not constricted at the throat.
    - Leaves densely covered with a silvery tomentum. 5. *E. crassifolium.*
    - Leaves clothed with a dull gray tomentum or sometimes nearly glabrous on the upper surface.. 5*a*. *E. crassifolium nigrescens.*
  - Calyx and corolla with stalked glands; corolla more or less constricted at the throat.
    - Stamens equaling the corolla tube, this slightly constricted at the throat ..... 6. *E. tomentosum.*
    - Stamens half as long as the corolla tube, this strongly constricted at the throat ..... 7. *E. Traskiae.*

Leaves sessile; herbage more or less hirsute..... 8. *E. sessilifolium.*

1. ERIODICTYON CALIFORNICUM (Hook. & Arn.). Torr. Bot. Mex. Bound. 148. 1859.

Wigandia californica Hook. & Arn. Bot. Beechy 364. 1840.
Eriodictyon glutinosum Benth. Bot. Voy. Sulphur 36. 1844.
Eriodictyon glutinosum var. *serratum* Choisy, DC. Prod. **10**:483. 1846.
Eriodictyon californicum forma *linearis* Brand, Univ. Calif. Pub. Bot. **4**:224. 1912.
Eriodictyon californicum subsp. *glutinosum* Brand, in ENGLER, Pflanzenreich **59**:141. 1913.
Eriodictyon californicum forma *latifolia* Brand, *loc. cit.*

An erect shrub 1–3 m. high, with mostly erect branches, the older branches and trunk clothed with light brown shreddy bark, the branchlets glabrate and glutinous, terete or sometimes angled: leaves lanceolate or oval, sometimes linear-lanceolate, 4–10 cm. long, 1–5 cm. wide, dentate or undulate, glabrous and glutinous above, whitened beneath with a fine indument between the reticulations, the midvein prominent, its main branches usually anastomosing at the margin; petioles gradually narrowed to the base, sometimes winged: branches of the inflorescence glabrous: sepals with a few scattered hairs or glabrous, linear, $\frac{1}{3}$ as long as the corolla: corolla funnelform, about 12 mm. long: stamens unequal, in sets of three long and two short or sometimes the reverse: style half as long as the corolla tube: capsule globular, usually covered with a white gum: seeds brown, about 6–12 maturing in a capsule.

BRAND's two forms, *latifolia* and *linearis*, may occur in almost any locality where plants are subjected to different exposures. They are adjustments of the individual to local environmental conditions, and are not worthy of a taxonomic designation.

TYPE LOCALITY.—Described from specimens collected by DOUGLAS in the coastal region of central California, between Sonoma and Monterey.

DISTRIBUTION.—Inhabits the Upper Sonoran and Lower Transition zones, growing on clay, sandy, or rocky soils. Ranges from the southern end of the Sierra Nevada in Kern County and the Coast Ranges of San Luis Obispo County northward to the Siskiyou Mountains, where it reaches its northern limit, so far as known, in the vicinity of Wimer, Jackson County, Oregon. In the central Sierra Nevada it has been collected well within the Transition zone in Yosemite Valley (*Abrams* 4563) between Mirror Lake and Kenneyville, but associated with a number of other Upper Sonoran intruders. In the coastal

region it is seldom met with in the fog belt or typical redwood region, or again on the dry hot eastern slopes of the Inner South Coast Ranges.

SPECIMENS EXAMINED.—Oregon, Jackson County: Wimer, *Hammond* 291; Dunn's Butte, near Ashland, *Walpole* 250. Josephine County: Waldo, *Piper* 6215.

California.—Siskiyou County: hills west of Yreka, *Heller* 7996; dry thickets, near Yreka, *Butler* 1405. Humboldt County: Hupa Indian Reservation, alt. 500 ft., *Chandler* 1352; between Three Rivers and the mouth of Willow Creek, *Tracy* 3360. Mendocino County: near Cummings, *Davy* and *Blasdale* 5336; Round Valley, alt. 400 m., *Chestnut* 165; near Ukiah, *Bolander* 3912; *Purdy*, 1897. Tehama County: Cooper's South Fork of Elder Creek, *Ward* 108; Fort Reading, *Newberry*. Colusa County: College City, *Miss King* 1905. Butte County: Butte Creek, *Mrs. Austin* 1811; Little Chico Creek, *Mrs. Austin* 296. Plumas County: Shoo Fly Bridge, *Mrs. Austin*, August 1893. Lake County: Eel River, one mile below Hullville, *Heller* 6032; Clear Lake, *Torrey*, 1865. Sonoma County: Little Sulphur Creek, *M. S. Baker*, June 11, 1898. Marin County: Mount Tamalpais, *Michener* and *Bioletti*, May, 1892; *Eastwood*, May 30, 1898; Bolinas Ridge, *Palmer* 2339. Solano County: Putah Bluffs, *Jepson*, May 1891; Gates Cañon, near Vacaville, *Heller* and *Brown* 5380. Contra Costa County: northeast of Mount Diablo, *Brewer* 1133; southeast of Mount Diablo, *Brewer* 1158; Antioch, *Brandegee*, June 1908. Alameda County: Oakland, *Chestnut*. San Mateo County: Belmont, *Davy*, June 17, 1893; Lake San Andreas, *Elmer* 4801; King's Mountain road, *Miss Randall* 164; Searsville Ridge, *Dudley*, June 4, 1895. Santa Clara County: hillsides near Stanford University, *Dudley*, April 1893; between Saratoga and Los Gatos, *Dudley*, April 16, 1893; Black Mountain, *Rutter* 8; foothills west of Los Gatos, *Heller* 7384; near Stanford University, *Abrams*, May 1898, May 1901. Santa Cruz County: upper part of San Lorenzo road near the river, *Dudley*, May 7, 1893; Glennwood, *Horace Davis*, September 1907; Boulder Creek, *Bailey*, October 13, 1891; Soquel Gulch, *Mrs. B. H. Thompson*, June 7, 1902; Lorenzo Cañon, *Mrs. B. H. Thompson*, July 6, 1902. Monterey County: Monterey, *Parry*, 1850; Pescadero ranch, *Brewer* 670; near Mission Soledad, *Brewer* 583; Santa Lucia Mountains, *Plaskett*, May 1898; Tassajara, *Elmer* 3204. Calaveras County: Gwin Mine, *Jepson*, October 6, 1902. Amador County: Agricultural Station, alt. 2000 ft., *Hansen* 187; New York Falls, alt. 1500 ft., *Hansen* 1647; vicinity of Ione, alt. 200–500 ft., *Braunton* 102. Mariposa County: Mariposa, *Congdon*, June 1883; Yosemite Valley between Mirror Lake and Kenneyville, *Abrams* 4563; Kingsley, *Miss Hook*, May–June 1905. Madera County, Chiquito Creek, alt. 6000 ft., *Blethen*, June 30, 1912; North Fork and vicinity, *Griffiths* 4538. Tulare County: Giant Forest, *Brandegee*, August 1905. Kern County: North Fork of Kern River, alt. 750 m., *Coville* and *Funston* 1034; Kern River Cliffs, *Dudley* 767; vicinity of Havilah, *F. Grinnell* 275; Johnson's Cañon, Walker Basin, *F. Grinnell* 30, 116.

2. ERIODICTYON TRICHOCALYX Heller, Muhlenbergia **1**:108. 1904.

Eriodictyon angustifolium pubens Gray, Proc. Am. Acad. **17**: 224. 1882.

Eriodictyon californicum subsp. *australe* Brand, ENGLER; Pflanzenreich **59**: 141. 1913, in part.

Eriodictyon californicum var. *pubens* Brand, *loc. cit.*

Eriodictyon glutinosum var. *intermedium* Parish, Brand, *loc. cit.*, published as a synonym.

Low shrub 0.5–1.5 m. high, with the erect branches and branchlets glabrous or nearly so and glutinous: leaves broadly lanceolate to linear-lanceolate, 5–10 cm. long, 1–3 cm. wide, firm coriaceous, flat and dentate or sometimes slightly revolute, glabrous and glutinous on the upper surfaces, paler beneath with a close fine tomentum within the conspicuous reticulations: branches of the inflorescence pubescent: calyx densely pubescent, nearly equaling the corolla tube: corolla 5–6 mm. long, its tube funnelform, white, densely pubescent without.

This species was first described by GRAY as a variety of *angustifolium*, but afterward (**4**) considered by him as one of the intermediate forms between that species and *californicum*. BRAND, basing the distinction mainly on the relative length of the free and adherent parts of the filaments, considered it as a variety of *californicum*, and restored *angustifolium* to specific rank. That the species is closely related to both *angustifolium* and *californicum* is evident, but the tendency to approach *californicum* is not through intergradation with typical *californicum*, but with *crassifolium nigrescens*. It is through this variety that all three of the species, *californicum*, *crassifolium*, and *trichocalyx*, form almost a complete series of intergradations. With this as the status of these forms, as demonstrated now by a large series of specimens, there are two ways of expressing their relationship taxonomically, either *crassifolium*, *trichocalyx*, and *californicum* should be considered as strains of a single species, or each should be given specific rank, and their more extreme geographical forms varietal rank, admitting that they do have a tendency to intergrade in contiguous territory. We have chosen the latter course because relationship can be shown sufficiently accurate by the simple binomial and trinomial method without the introduction of such burdensome combinations as *Eriodictyon californicum australe pubens coarctatum* Brand. Such combinations are as cumbersome as the pre-Linnaean system and less significant, for they need not be in any way descriptive.

TYPE LOCALITY.—"Seven Oaks Camp, San Bernardino Mountains."

DISTRIBUTION.—This species grows in stony or sandy soil in the chaparral of the San Gabriel and San Bernardino mountains. It extends from elevations of 1000 ft. on the sandy plains of the San Gabriel and San Bernardino valleys

to 8000 ft. on the south slope of San Antonio Mountain, and to nearly the same altitude on the south side of the divide between Seven Oaks and Bear Valley. On the desert slopes of the mountains it has been collected as low down as the juniper belt along Rock Creek.

SPECIMENS EXAMINED.—Los Angeles County: Mount Wilson, alt. 5600 ft., *Abrams* 2607; Claremont, *Chandler*, May 11, 1897; Rock Creek, desert slopes of the San Gabriel Mountains, *Abrams* and *McGregor* 526; Mount San Antonio, alt. 8000 ft., *Abrams* 1939, 2607. San Bernardino County: Lytle Creek, San Gabriel Mountains, alt. 800 m., *Leiberg* 3335; near San Bernardino, *Vasey* 438; *Coville* and *Funston* 107; sandy plains, near Colton, *Pringle*, May 27, 1882; Hogback, San Bernardino Mountains, *Parish* 2977 (approaching *crassifolium nigrescens*); Holcomb Valley, San Bernardino Mountains, *Shaw* and *Illingsworth* 85; Victorville, *Hall* 6188. Riverside County: Banning, *Brandegee*, May 14, 1895; Whitewater, alt. 1126 ft., *Parish* 2976. Lower California: no locality, *F. E. Fish*, May 7, 1883 (this is herbarium sheet no. 45671 of the National Herbarium. The locality is not given and two labels are attached, one purporting to be ORCUTT'S and the other FISH'S, but neither is apparently original. The specimens are not in flower, but seem to belong here); near Ensenada, *Jones* 3739 (this plant together with a specimen collected by *Brandegee*, May 20, 1893, on San Pedro Martir Mountain, BRAND described as *californicum* subsp. *australe* var. *pubens* subvar. *coarctatum*. *Jones's* specimen may well be placed with *trichocalyx*, although the specimen at hand is too scrappy to warrant more than a guess, but *Brandegee's* specimen is strikingly different. It is much like typical *angustifolium* in foliage characters and size of flowers, but the filaments are a little more united to the corolla tube. In this respect it seems intermediate between *angustifolium* and *trichocalyx*).

3. **Eriodictyon lanatum** (Brand) Abrams, sp. nov.

Eriodictyon californicum subsp. *australe* var. *lanatum* Brand, in ENGLER, Pflanzenreich **59**:142. 1913.

An erect branching shrub, 0.6–2 m. high, with the branches more or less permanently tomentose: leaves thick coriaceous, slightly revolute on the entire, undulate or dentate margins, 2–7, mostly about 5, cm. long, 8–20 mm. wide, tapering from near the middle to both ends, glabrous and glutinous above, at least in age, densely covered beneath with a white tomentum obscuring the reticulations: branches of the inflorescence pubescent; flowers crowded in the scorpioid cymes: sepals densely white-pubescent, about 2.5 mm. long: corolla funnelform, 7–8 mm. long, much exceeding the calyx, pale purplish-blue or nearly white, the tube pubescent without.

TYPE.—The type of the variety is *Abrams* 3632, collected in chaparral between Campo and Jacumba. The description of the species is drawn from a sheet of the same collection deposited in the Dudley Herbarium.

DISTRIBUTION.—Southern California from the vicinity of Toro Mountain, Riverside County, southward through the chaparral region, especially on the desert slopes of the Cuiamaca Mountains, to the northern boundary of Lower California.

SPECIMENS EXAMINED.—Riverside County: near Toro Mountain, *Leiberg* 3199. San Diego County: Jacumba Hot Springs, *Mearns* and *Schoemfeldt* 3261, 3288; Mountain Springs, *Mearns* and *Schoemfeldt* 3207; Cameron's ranch, Laguna, *Mearns* and *Schoemfeldt* 3702; San Felipe, *Brandegee*, April 16, 1895; Colorado Desert, in the foothills, *Brandegee*, April 13, 1896; Potrero, *Alderson*, May 1893; Palm Creek, Colorado Desert, *Brandegee*, April 18, 1895; Laguna Mountains, *Brandegee*, June 20, 1904; in chaparral between Jacumbo and Campo, *Abrams* 3632; Campo, *Hall* 9424. Lower California: Nachoguero Valley, *Mearns* and *Schoemfeldt* 3463.

4. ERIODICTYON ANGUSTIFOLIUM Nutt. Jour. Acad. Nat. Sci. Phil. II. **2**: 181. 1848.

Eriodictyon glutinosum angustifolium Torr., GRAY, Syn. Fl. **2**:176. 1878.

Low erect shrub, 0.6 to 2 m. high, the branches often crowded, glabrous and glutinous: leaves narrowly linear to narrowly linear-lanceolate, 5–10 cm. long, 3–10 mm. wide, entire or inconspicuously dentate, revolute, glabrous and glutinous above, canescent and reticulated beneath: branches of the inflorescence glabrous and glutinous or sparsely pubescent: cymes racemosely or corymbosely arranged: sepals linear, nearly glabrous or somewhat hirsute: corolla nearly campanulate, its tube only about 5 mm. long, not exceeding the calyx: filaments united only $\frac{1}{3}$ their length: seeds black, slightly longer than those of *californica*.

TYPE LOCALITY.—"On the Sierra of Upper California [Arizona]."

DISTRIBUTION.—In the Upper Sonoran chaparral of southern Nevada and southern Utah southward through Arizona, and also in Lower California in the San Pedro Martir region.

SPECIMENS EXAMINED.—Utah: Silver Reef, alt. 3500 ft., *Jones* 5149, 5176; nearly at the head of the grade 5 miles above Bellevue, *Jones* 5001; Sandy, 4 miles east of Leeds, alt. 3400 ft., *Jones* 5214. Nevada: Charleston Mountains, alt. 4000–5000 ft., *Purpus* 6074; Bunkerville, Virgen River, *Goodding* 746. Arizona: Diamond Valley, *Purpus*, May–October 1898; "hills near Cactus Pass in the western part of New Mexico" (probably in western Arizona on Bill Williams Fork), *Bigelow*, 1853; Pinal Mountains, *Jones*, May 24, 1890;

Oak Creek, *Rusby* 239; no locality, *Palmer*, 1869; Santa Catalina Mountains, *Lemmon*, May 1881; Copper Basin, *Toumey* 199-*b*; Cheno Valley, *Toumey* 199-*a*; canyon 2 miles below Pagumpa, alt. 4000 ft., *Jones* 5089. Lower California: Trinidad Valley, *Belding*, May 1885; Vallederos Creek, *Brandegee*, May 29, 1893; San Pedro Martir Mountain, *Brandegee*, May 4 and 20, 1893.

5. ERIODICTYON CRASSIFOLIUM Benth. Bot. Voy. Sulph. 35. 1844.

Eriodictyon tomentosum of various authors, not Benth.

Eriodictyon crassifolium subsp. *Grayanum* Brand, in ENGLER, Pflanzenreich 59:139. 1913.

Eriodictyon crassifolium var. *typica* Brand, *loc. cit.*

Shrub 1–4 m. high, with spreading branches, the twigs, both surfaces of the leaves, and calyx densely hoary or silvery tomentose: leaves 7–15 cm. long, 2–5 cm. wide, reticulate beneath, not revolute, entire or crenate, dentate or sometimes shallowly lobed: sepals about 5 mm. long, narrowly linear: corolla 10–15 mm. long, rather broadly funnelform, pale bluish purple, pubescent without: seeds smaller than in *californicum* and indented.

TYPE LOCALITY.—"San Diego."

DISTRIBUTION.—Typical *crassifolium* inhabits the dry gravelly or sandy mesas and foothills in the vicinity of San Diego and extends northward to Santiago Canyon, Santa Ana Mountains, in the coastal region, also on the mesas and foothills between the Santa Ana and the San Jacinto mountains, where it extends to the desert slope in the vicinity of Palm Springs. In the Los Angeles region, extending along the coastal slopes of the San Gabriel Mountains to the Santa Monica and San Fernando mountains, the leaves are covered with a somewhat less dense and shorter tomentum, giving a dull gray instead of a hoary tone. These plants often have the flowers reduced in size and grade fairly gradually into the variety *nigrescens*. This more or less intermediate type extends on northward to the Tehachapi region.

SPECIMENS EXAMINED.—Kern County: San Emidio Canyon, *Davy* 2026; San Emidio Potreros, alt. 5000 ft., *Hall* 6391; vicinity of Fort Tejon, *Xantus de Vesey* 94; Canada de las Uvas, alt. 1050 m., *Coville* and *Funston* 1142. Los Angeles County: Mount Lowe, *Grant* 417; Little Santa Anita Canyon, *Abrams* 2627; San Fernando Mountains, near Chatsworth, *Abrams* 1363; Santa Monica Mountains, *Hasse*, June 1892; Los Angeles, *Brewer* 39; Glendora, *Braunton* 293. Orange County: Santiago Canyon, *Miss Bowman*, June 1899; *Hall* 9402. Riverside County: western base of the San Jacinto Mountains, *Hall* 2006; Hemet, *Hall* 561; Valle Vista, San Jacinto Mountains, *Hall* 1107; Elsinore, *Abrams* 5052; Tahquitz Canyon, near Palm Springs,

Dudley, December 25, 1903; near San Jacinto, *Leiberg* 3214; *Berg*, April 3, 1904; Menifee, *Miss King*, 1893. San Diego County: San Diego, *Barclay* (type); *Cooper* 498; *Palmer*, 1875; *Pringle*, April 26, 1882; *Dunn*, April 21; *Jones* 3143; Mission hills, near San Diego, *Abrams* 3432; Point Loma, *Chandler* 5067 (this specimen resembles the less tomentose form of the Los Angeles region, a condition undoubtedly due to the greater humidity on the promontory than on the adjacent mainland); Encinatas, *Brandegee*, March 28, 1894; Witch Creek, *Alderson*, April 1894; San Ysabel, *Henshaw* 148; near Bennington, *Dudley*, January 1908.

5*a*. ERIODICTYON CRASSIFOLIUM NIGRESCENS Brand, in ENGLER, Pflanzenreich **59**: 140. 1913.

Leaves smaller and comparatively narrower, dull gray green with a shorter and much less dense tomentum, usually crenate-dentate: corolla narrowly funnelform, about 6 mm. long, white and densely hairy without.

This variety is intermediate between *crassifolium* and *trichocalyx*. The intergradation with typical *crassifolium* is complete but less marked with *trichocalyx*, although the form originally described by GRAY as *angustifolium* var. *pubens* partakes of both and might be placed in either category.

TYPE LOCALITY.—Acton, Los Angeles County.

DISTRIBUTION.—Chaparral-covered slopes of the Liebre and San Gabriel mountains, especially in the Soledad Pass region.

SPECIMENS EXAMINED.—Acton, *Elmer* 3596, 3598; Kings Canyon, Liebre Mountains, *Dudley* and *Lamb* 4343; Oakgrove Canyon, Liebre Mountains, *Abrams* and *McGregor* 322.

5*b*. ERIODICTYON CRASSIFOLIUM **denudatum** Abrams, var. nov.

Leaves 10–15 cm. long, 2–3.5 cm. wide, flat and more or less dentate on the margins, green and glabrate but not evidently glutinous on the upper surface, soft tomentose beneath, as also the branches and inflorescence: calyx densely clothed with silky hairs, about one-third the length of the corolla tube: corolla lavender, densely pubescent without, 8–10 mm. long.

This variety is the extreme type of the *crassifolium* group; it merges into the variety *nigrescens* and through the Los Angeles form into typical *crassifolium*, while the denuded upper surface of the leaves suggest close affinity with *californicum*. It occurs in the cross ranges of Santa Barbara and Ventura counties, the region from whence *californicum*, *crassifolium*, and *trichocalyx* diverge. It is natural, therefore, according to the Jordan law, that we should find here the intermediate forms.

TYPE.—Red Reef Canyon, Topatopa Mountains, alt. 2800–3500 ft., Ventura County, California, *Abrams* and *McGregor* 159, June 8, 1908. The type sheet is deposited in the Dudley Herbarium of Stanford University.

DISTRIBUTION.—Chaparral-covered hills and mountains of Santa Barbara and Ventura counties.

SPECIMENS EXAMINED.—Santa Barbara County: Santa Inez Mountains, near Santa Barbara, *Brandegee*, 1888. Ventura County: Ojai and vicinity, *Peckham*, April 13, 1866; Sisar Canyon, Topatopa Mountains, *Abram* and *McGregor* 65; Red Reef Canyon, Topatopa Mountains, *Abrams* and *McGregor* 142, 159. Kern County: Vicinity of Fort Tejon, *Abrams* and *McGregor* 300 (approaches the Los Angeles form of *crassifolium*).

6. ERIODICTYON TOMENTOSUM Benth. Bot. Voy. Sulph. 36. 1844.

Eriodictyon niveum Eastw. Proc. Cal. Acad. III. 1:130. 1898.

Eriodictyon crassifolium subsp. *Benthamianum* var. *niveum* Brand, in ENGLER, Pflanzenreich **59**:140. 1913.

An erect, branching shrub with the herbage hoary throughout with a dense feltlike tomentum or rarely becoming more or less denuded and green: leaves thick, elliptic-ovate or obovate, 4–6 cm. long, 1–3 cm. wide, cuneate at base, acute or obtuse at apex, entire, crenate, or even coarsely dentate, veins scarcely evident on the upper surface, beneath reticulate-rugose; panicle terminating a usually elongate naked peduncle widely branched or simple; flowers crowded, nearly sessile: calyx lobes linear-subulate, equaling the corolla tube, clothed with white silky hairs with a few stalked glands interspersed: corolla white or pale violet, 4 mm. long, urceolate, glandular-hirsute without, the tube slightly contracted below the very short spreading lobes: stamens with the free portion of the filaments short, inserted below the throat; anthers oval 1 mm. long.

Until now the identity of *E. tomentosum* has been misunderstood. TORREY (9) first considered it and *crassifolium* as conspecific, with the remark, "We have specimens that are intermediate and Dr. PARRY informs me that he has seen them in California passing into each other." We have failed to find in the field or in any of the herbaria any intermediate forms, nor is there any evidence that PARRY ever collected true *tomentosum*. Geographically and structurally, aside from the superficial character of hoariness, these two species are more distinct than *crassifolium* and *californicum*. TORREY'S conclusions were followed by GRAY and other botanists until GREENE (6) discovered a plant in Monterey County which he believed to be the true *tomentosum*.

Miss EASTWOOD, red scovering the same plant and wishing to solve the problem, sent specimens of her Monterey plant and also *crassifolium* material from San Diego to Kew to be compared with the types. The person at Kew who investigated the matter for her replied that "*Eriodictyon crassifolium* and *E. tomentosum* are conspecific, and your plant is apparently an undescribed species." This seemed final, but from our distributional studies we found that the northern limit of true *crassifolium* is far south of the region visited by DOUGLAS, who first collected *tomentosum*. We know that DOUGLAS collected in the vicinity of Mission San Antonio where *niveum* is found, and about Santa Barbara where *Traskiae* and *crassifolium denudatum* grow. Which of these was the true *tomentosum* was not evident without access to the type, but that one of them and not *crassifolium* would prove to be it seemed probable. We wrote, therefore, to Dr. OTTO STAPF, of the Kew Herbarium, who furnished us with a photograph of the type of both *crassifolium* and *tomentosum*, and also fragments for study. The evidence was clear; *tomentosum* and *niveum* were found to be one and the same.

TYPE LOCALITY.—Not given in the original publication, but collected by DOUGLAS probably in the vicinity of Mission San Antonio, Monterey County.

DISTRIBUTION.—On the chaparral-covered eastern slopes of the Santa Lucia Mountains, extending southward through the middle foothill region of Monterey and San Luis Obispo counties.

SPECIMENS EXAMINED.—Monterey County: without locality but probably from the Jolon region, *Douglas* 1833; Jolon, *Vasey* 439; *Mrs. K. Brandegee*, June 8, 1909; Tassajara Hot Springs, *Elmer* 3210; San Antonio Creek, above the Mission, *Dudley*, May 11, 1895; Cholome, *Lemmon;* Arroyo Seco, Santa Lucia Mountains, *Dudley*, January 1, 1896; China Camp, on road to Tassajara Hot Springs, alt. 3500 ft., *Cox*, July 1908; near Soledad, *Congdon*, June 1881. San Luis Obispo County: between Pozo and La Panza, *Miss Eastwood*, June 10, 1902; Santa Margarita Mountains, east of pass on road to San Luis Obispo, *Dudley*, April 3, 1903; central coast ranges, *Palmer*, 389.

7. ERIODICTYON TRASKIAE Eastw. Proc. Cal. Acad. III. 1:131. 1898.

Eriodictyon crassifolium subsp. *Benthamianum* var. *Traskiae* Brand, in ENGLER, Pflanzenreich **59**:140. 1913.

An erect branching shrub 1–2 m. high, clothed with a hoary feltlike tomentum except on the calyx: leaves oblanceolate to elliptic-ovate, 5–12 cm. long, 1.5–4 cm. wide, acute at apex, narrowed at base to a petiole 1 cm. long or more, dentate, veins obscure on the upper surface, reticulate-rugose beneath: panicle usually much branched, bearing short congested terminal cymes, or these elongated; flowers short-pediceled, crowded: sepals

narrowly linear, 4–5 mm. long, dark colored, and glandular-hirsute: corolla purple, the tube equaling the calyx, contracted at the throat and base: the lobes irregularly orbicular, these and the upper part of the tube glandular-hirsute without: stamens inserted in the middle of the tube, nearly sessile: ovary glandular-hirsute.

This species is closely related to *tomentosum* and possibly should be considered a variety. The two are best differentiated by the position of the stamens.

TYPE LOCALITY.—"On one volcanic upland on Santa Catalina Island, California, at an elevation of about 1500 feet."

DISTRIBUTION.—Santa Catalina Island and on the mainland in the Santa Inez Mountains, Santa Barbara County. Why it should occur in practically unmodified form on the mainland and the islands is not easily explained, although the fact that it is found on the islands in only one station and that composed of only a few bushes would indicate that it had been transported, possibly by birds of passage, from the mainland. It is significant in this connection that a number of insular species are also found on the mainland in the Santa Barbara region.

SPECIMENS EXAMINED.—Santa Barbara County: Painted Cave ranch, *Eastwood*, May 9, 1908; Sisquoc, *M. S. Baker*, July 1895; La Cumbre trail, Santa Inez Mountains, *Abrams* 4311; Santa Inez Mountains, *Eastwood*, May 17, 1904; *Hall* 7845; bushy hills, head of Santa Inez River, *Hall* 7830; near Santa Barbara, *Brewer* 296; *Elmer* 4017; *Brandegee*, 1888. Los Angeles County: Santa Catalina Island, *Blanche Trask*, May 1897 and September 1910.

8. ERIODICTYON SESSILIFOLIUM Greene, Bull. Cal. Acad. Sci. 1:201. 1885.

A shrub 1–2 m. high with very leafy glandular-pubescent and hirsute branches: leaves lanceolate-oblong, 6–12 cm. long, 2–4 cm. wide, acute at apex, sessile and truncate or cordate-clasping at base, coarsely serrate, glutinous and nearly glabrous to densely hirsute on the upper surface, sparsely to densely hirsute beneath and short-tomentose between the veins: inflorescence an open or somewhat congested cymose panicle: sepals villous-hirsute and glandular, about 5 mm. long: corolla funnelform, 12 mm. long, lilac-purple, pubescent without but not glandular: stamens equal, their filaments densely clothed with bristly hairs: capsule globular: seeds dark brown or nearly black.

Considerable variation in the amount of hirsute pubescence suggests a plastic condition or possibly two varietal strains, but too few collections have

been made and too little is known of its geographical range to warrant any new propositions to designate these forms.

TYPE LOCALITY.—"All Saints Bay, Lower California."

DISTRIBUTION.—On canyon slopes in the coastal region of northern Lower California, especially in the neighborhood of Ensenada.

SPECIMENS EXAMINED.—Lower California: Todas Santas, *Fish*, June 2, 1883; La Gruella Canyon, *Orcutt*, July 14, 1885; Guadaloupe Canyon, *Orcutt*, January 20, 1882, and June 2, 1883; Burro Canyon, *Brandegee*, April 22, 1893.

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CALIFORNIA

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GAMETOPHYTE OF PELLIA EPIPHYLLA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 206

A. H. HUTCHINSON

(WITH PLATES I–IV AND ONE FIGURE)

Three of the species of *Pellia*—*P. epiphylla*, *P. calycina*, and *P. endivaefolia*—show morphological differences, especially with respect to the apical cell, which would suggest a generalized or possibly an unstable ancestral form. No detailed study of any of these species has been reported. During the investigation upon which this account is based, it has been found that in *P. epiphylla* not only are there transitions in the method of growth, but also that the development of the antheridium may follow any one of several divergent lines.

Antheridium

It has been generally accepted that "the antheridium of *Pellia* is larger than that of *Aneura*, but its development is very similar, except that the stalk is multicellular, as it is in other *Anacrogyneae*."[1] In addition to this method of development, *P. epiphylla* shows young antheridia having characters of Marchantiales; moreover, the spermatogenous initials may be cut out in the same way as the primary axial cell of the archegonium.

The division of a dorsal cell, the third or fourth from the apical cell, by a horizontal cross-wall is the first evidence of an antheridial initial. The outer of the two cells formed divides again, giving the three cells of the antheridial row—the basal cell, the stalk initial, and the outer cell; the latter by successive divisions gives rise to the wall cells and spermatogenous cells. Meanwhile, the dorsal cells, immediately surrounding the antheridial group, divide and become papillate, thereby producing a ring-shaped involucre (figs. 2, 3). The outer cell of the antheridial group divides next. The position of the wall is significant; if it is vertical and median,

[1] CAMPBELL, D. H., Mosses and ferns. New York. 1905 (p. 92).

the successive divisions follow an antheridial sequence; if, however, the wall is inclined and somewhat removed from the central position, the cell divisions which follow are similar to those of a developing archegonium. In the former case the vertical wall is followed by a curved wall on either side, which cuts the vertical wall as shown in figs. 7 and 8. Two similar walls, rotated about the central axis through an angle of 90° (figs. 8, 9), complete the separation of the peripheral region from the central spermatogenous region. The first two of these walls may be nearly parallel at the base (fig. 7), or they may be at right angles; similarly the second pair. Such an antheridium is characteristic of the Jungermanniales.

Occasionally the outer cell, mentioned above, is divided into quadrants by walls at right angles to the vertical wall (figs. 10, 11), in which case four wall cells are cut off by periclinal divisions, giving also four spermatogenous cells. The process is similar to that characteristic of *Sphaerocarpus* or Marchantiales.

Fig. 14 illustrates the result of a combination of these two methods of development. In fig. 15 is shown a double antheridium; the two halves have become completely separated by the vertical division and each has developed independently. The process may be compared to the characteristic development of the double antheridia of Anthocerotales.

When the first wall formed in the outer cell is inclined and somewhat removed from the median position, it is followed by a second and a third wall, each of which is similarly placed, but revolved with respect to each other through an angle of 120° about the vertical axis (figs. 17, 18, 26, 27, 28). A transverse wall divides the central cell into the cap cell and the spermatogenous initial (fig. 19). The characteristic archegonial development is followed until the massive spermatogenous group begins to be formed (figs. 22, 28), instead of the axial row.

Occasionally this critical third wall of the antheridium is inclined inward instead of outward, as described above (fig. 23). Two walls similarly inclined complete the separation of the peripheral region from the central spermatogenous initial (figs. 24, 25). This form is similar to that last described with the exception of the inclination of the walls and the resulting lack of the cap cell.

The differences in these antheridia are emphasized by the fact that in the first form (fig. 8) there are two spermatogenous initials, paired as in Jungermanniales; in the second form there are four, arranged in the form of a quadrant (fig. 10), as in Marchantiales; and in the third and fourth there is but one spermatogenous initial (figs. 10, 24, 25).

That the structures described above are developing antheridia, and not archegonia, is evidenced by their position and by the presence of an individual involucre. The antheridia are single and dorsal, while the archegonia are grouped in the terminal pocket.

Archegonium

The position of the archegonial group is of considerable morphological importance. CAMPBELL, with reference to the work of JANCZEWSKI, states: "The archegonia are formed in groups just back of the apex but he [JANCZEWSKI] does not seem to have been able to detect any relation between them and the apical cell such as obtains in *Aneura*, but it is possible that such a relation does exist." As mentioned above, the archegonia are terminal and inclosed in a "pocket," which is formed by a cup-shaped involucral growth. As will be described more fully, the archegonia arise from an apical group of cells, any of which may become an archegonium initial. There is no regular succession in the formation of archegonia; apparently old and young organs are indiscriminately intermingled. Since the apical group ceases to function as such after the production of archegonia, *P. epiphylla* may be regarded as truly acrogynous. The involucre is produced by cells which are cut off laterally by the apical group (fig. 40), and pushed out very much as the wings during the previous period of growth; in this event, however, the lateral cells are forced out on all sides to form a complete inclosure.

The structure and development of the archegonium conforms, in general, to the characteristic liverwort form. Some specific characters may be noted.[2] "After the archegonial mother cell is cut off it does not divide at once by vertical walls, but a pedicel is first cut off [fig. 31]; after which the upper cell undergoes the

[2] CAMPBELL, D. H., Mosses and ferns. New York. 1905 (p. 90).

usual divisions." This character serves to emphasize the similarity which exists between the archegonium as shown (figs. 31–33), and the antheridium (figs. 16–21). Except for the position and presence or absence of the involucre, these organs would be difficult to differentiate until the spermatogenous group or the archegonial axial row, as the case may be, begins to develop. The cap cell gives rise to a group consisting of more than the usual number of cells. The first division of the cap is often simultaneous with the division which gives rise to the primary neck canal cell and the primary ventral cell (figs. 32, 35), and four cap cells may appear in cross-section when there are but three neck canal cells and a ventral cell (fig. 36). Fig. 38 shows a group of cap cells, 6 in cross-section, which may be compared with those which form the neck of the archegonium of Filicineae. JANCZEWSKI reports that the number of neck canal cells may be as high as 16 or even 18; 9 is the greatest number seen by the writer (fig. 38). The venter becomes massive before fertilization; it may be 2 or 3 cells in thickness; a many-celled stalk is also formed (fig. 37). In the young archegonium the neck has usually only 5 vertical rows of cells. The cells originating from the third wall cell do not divide until the archegonium approaches maturity (fig. 39).

Methods of growth

A certain form of apical cell may usually be given as characteristic of a genus or even of a larger group. In *Pellia*, however, there is no such conformity; the apical cell of *P. calycina* has four cutting faces, two lateral, a dorsal, and a ventral—the cuneate apical cell. The dolabrate apical cell of *P. endivaefolia* has but two cylindro-convex cutting faces; while that reported as characteristic of *P. epiphylla*, the lenticular cylindric apical cell, has a posterior convex and two lateral cutting faces. In the last named species, however, there are several methods of growth; these cannot be sharply delimited, but for clearness five rather distinct forms may be taken as characteristic of successive periods of growth.

During the time of intra-capsular gametophytic division a massive body is formed. There is no regional growth, but all cells have an equal power of division. This period of growth is of short

duration. The gametophyte body retains this massive form until after the resting period.

The second period of growth begins by the formation of a cuneate apical cell. A terminal cell is cleft by a wall inclined about 30° with reference to the longitudinal axis of the spore; a second inclined wall bisects the first at an angle of approximately 90°; lateral walls complete the cuneate apical cell (fig. 41). The latter cuts off dorsal and ventral segments (fig. 42) as well as lateral segments (fig. 43). Such a method of growth is characteristic of the young gametophyte until about the time of antheridium formation.

The growth of the third period is by means of a lenticular cylindric apical cell (fig. 47). The transition is somewhat irregular. Sometimes the apical cell is more or less equally divided; then the two halves simultaneously cut off cells (fig. 45) which correspond to the dorsal and ventral segments of the preceding form. The thallus in cross-section has the appearance of being medianally divided by a wall. Another transition form is shown in fig. 44. As the thallus becomes thicker the posterior angle becomes greater, the two faces being finally replaced by one which is curved. The cells cut off from the posterior face divide rapidly; as many as 6 segments may be formed before the next division occurs. The rapid division of the laterally placed cells causes the wings to be protruded outward and forward (figs. 46, 48, 49). There has been much discussion regarding the method of branching. HOFMEISTER[3] believed that the central papilla ("Mittellappen") shown in fig. 14 was the seat of the chief apex; hence that there is no true dichotomy. LEITGEB[4] states that the origin of the central papilla is from a marginal cell. When branching takes place, the apical cell, instead of cutting off a lateral segment, divides equally or almost so; each of these daughter cells assumes apical characters. The central papilla is produced by the crowding together of lateral segments from the two apical cells. It later develops into a central lobe corresponding to fused wings. Branching is essentially

[3] HOFMEISTER, W., Higher Cryptogamia. Ray Society. 1862.

[4] LEITGEB, H., Untersuchungen über die Lebermoose. 1882. Vols. II and III. Jungermannieen.

dichotomous; although the thallus may appear to have a central axis along the main line of growth, it is a matter of comparative rapidity in growth rather than origin. This form of apical cell is continued throughout the antheridial period.

The fourth period of growth is terminal and regional; it is concerned with the production of the archegonial pocket. The cells surrounding the original apical cell assume the power of cutting off lateral and posterior segments. The region of growth is in the form of a terminal disk. Lateral segments are crowded out on all sides to produce the continuous, cup-shaped involucre. A cross-section in any plane is similar to a horizontal section through the growing region at the time of branching (fig. 49). This growth is checked by the production of archegonia; any of the surface cells of the pocket may produce an archegonium (fig. 40). About the time of fertilization the last period of growth begins.

Any further growth is in connection with the developing sporophyte. Starch accumulates in the cells surrounding the foot and a massive growth takes place. Usually only one sporophyte develops in each pocket; a rather thick calyptra is formed about it, and sterile archegonia are carried along; these are to be seen attached to the surface of the calyptra. The first growth of the gametophyte is massive, similarly the last.

Relation of antheridium and archegonium

The relationship of the various forms of antheridia and their relation to the archegonium is demonstrated by the occurrence of antheridia in a single species, *Pellia epiphylla*, which are similar in development to each of these organs. The Marchantiales condition is generally to be found among the first antheridia; the Jungermanniales form is most dominant at the middle period, occurring, however, throughout the complete antheridial period. The archegonial form is usually found among the last antheridia to be produced. There is an evident time relation between these forms. Moreover, one may be regarded as derived from another through a series of progressive sterilizations (text fig. 1).[5] In the form

[5] Cf. HOFMEISTER, The higher Cryptogamia. Untersuchungen über die Lebermoose. Vol. II (*Pellia*).

characteristic of Marchantiales (figs. *A*, *B*, *C*), the vertical median wall (1) is followed by two walls (2 and 3) at right angles to the former, thereby forming quadrants (*A*, *B*, *C*, *D*). Four periclinal walls (4, 5, 6, 7) form a sterile wall cell and a spermatogenous cell

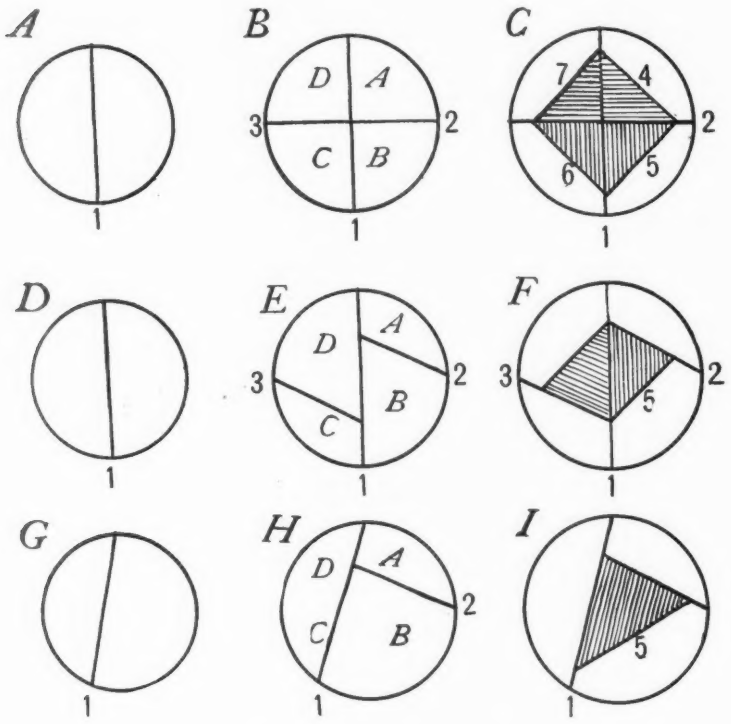


FIG. 1.—Explanation in text

from each quadrant. In the Jungermanniales form (figs. *D*, *E*, *F*) the median vertical wall is followed by two walls corresponding to the second and third above, but somewhat inclined (2, 3, fig. *E*). Periclinal walls (5, 7) form two centrally placed spermatogenous cells. The quadrants *A* and *C* have become sterile wall cells; only the quadrants *B* and *D* give rise to spermatogenous cells. In the

archegonial form (*G*, *H*, *I*) the first wall (1) is not median, but somewhat laterally placed and inclined; there is no wall no. 3; the section corresponding to the quadrants *C* and *D* does not divide, but remains as a sterile wall cell. Wall 2 again cuts off a section corresponding to quadrant *A*, which also persists as a sterile wall cell. A periclinal wall (5) divides the section corresponding to quadrant *B* into a wall cell and a spermatogenous cell. Three of the quadrants have become sterile. Starting with the Marchantiales form of antheridia, by the sterilization of alternate quadrants the Jungermanniales form is derived; and by the sterilization of three quadrants the archegonial form results. The sterilization sequence corresponds to the time sequence as described above.

Only one step is lacking in this series to complete the transition from the antheridium of Marchantiales to the archegonium, namely the reduction of the spermatogenous mass into a single row of cells, only one of which, the egg, shall be functional. Such transition forms have been described by DAVIS[6] in Marchantiales. The writer has seen such "archegonia" with gamete masses in sections prepared by Dr. W. J. G. LAND. *The antheridial forms of P. epiphylla furnish evidence that the various types of antheridia and the archegonium have had a common origin*, possibly gametangia resembling in structure the antheridium of Marchantiales.

Relationships

The genetic relationships of *P. epiphylla*, because of its diversity, present a rather complex problem. With respect to its relation to other species of the genus *Pellia*, if the other species retain throughout life the form of apical cell ascribed to them, it would follow that *P. epiphylla* has branched sooner from the general line of progress and has retained and developed generalized characters. As a member of the Jungermanniales, this species is acrogynous in the sense that growth is checked, apical growth is stopped, by the production of archegonia. It differs from the more characteristic Acrogynae in having several regions of growth, each of which is checked in the same way. It is possible that acrogyny

[6] DAVIS, B. M., The origin of the archegonium. Ann. Botany **17**: 477–492. 1903.

has been reached by several lines of development; hence close relationship with "Acrogynae" is not necessarily implied. If the development of the antheridium may be taken as a basis of classification, it would seem that *Pellia* arose from the main line of advance before the two branches, Jungermanniales and Marchantiales, became separate, even before the archegonium and antheridium became definitely differentiated in their methods of development.

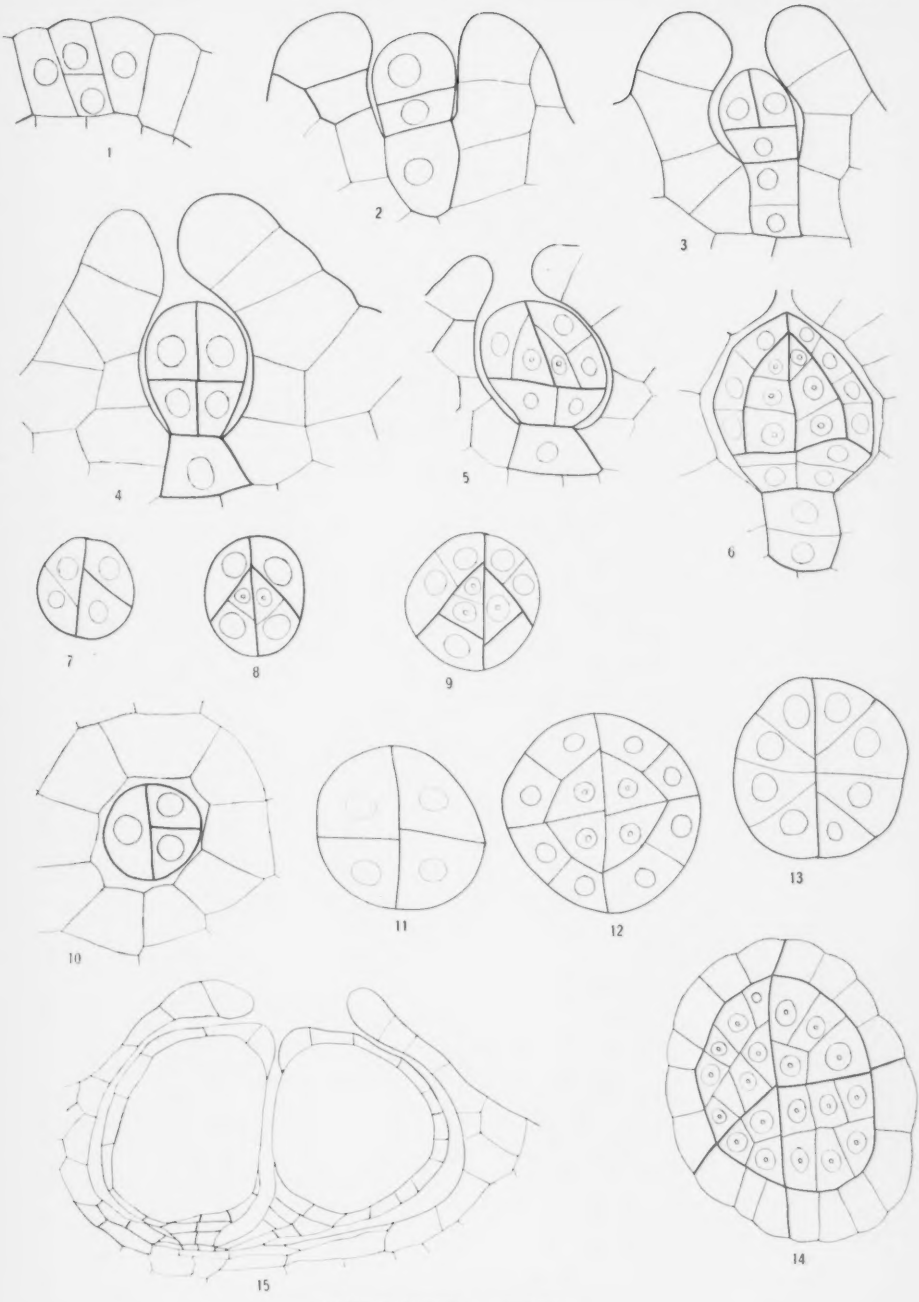
From *Pellia* we have evidence regarding the relation of Jungermanniales and Marchantiales. There is in the life history a transition from the cuneate apical cell of Marchantiales form to the lenticular cylindrical apical cell found in certain Jungermanniales; similarly, the antheridium, already discussed, affords strong evidence for the existence of such a relation. The evidence tends to indicate that Marchantiales are primitive and that Jungermanniales are derived.

Summary

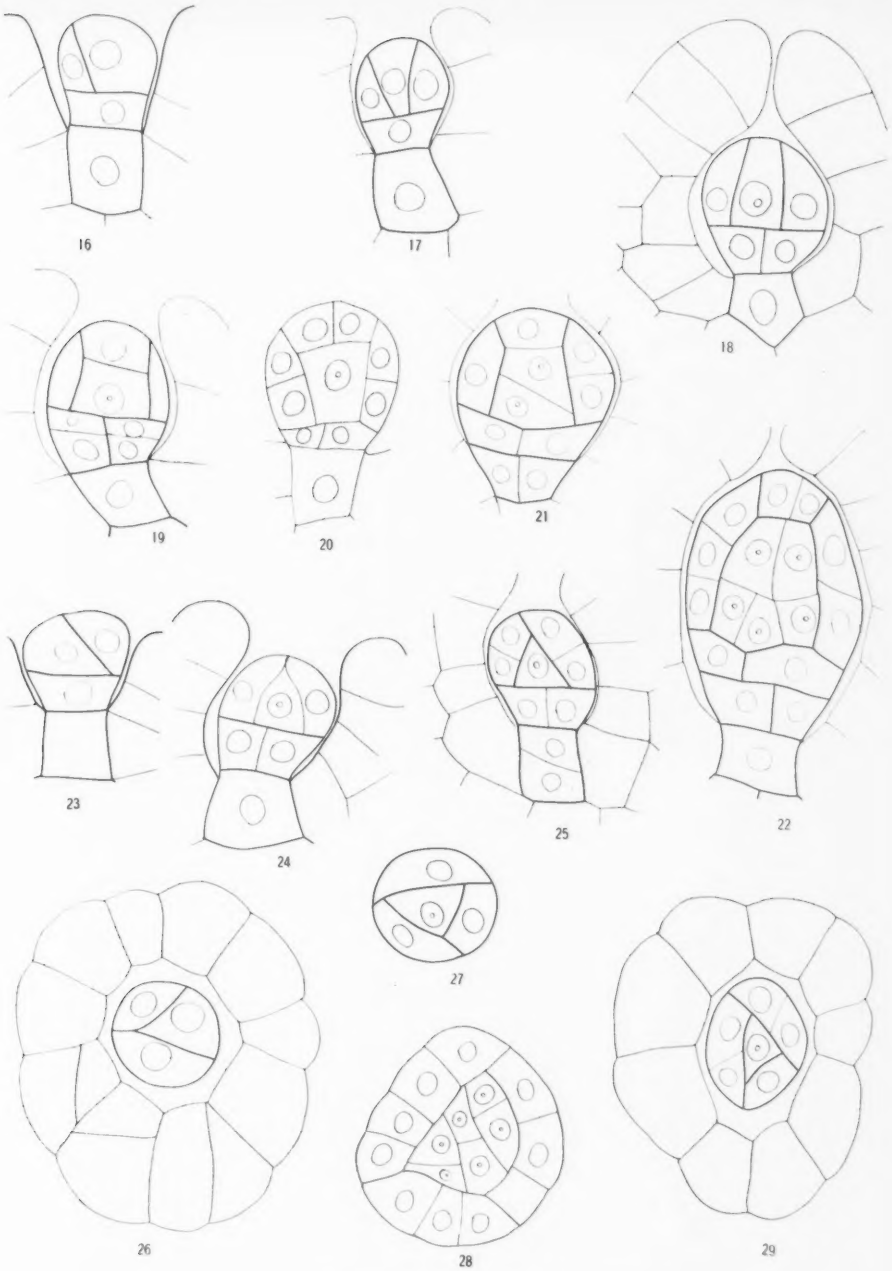
The antheridium.—The development varies. The dominant method is that characteristic of Jungermanniales; forms occur, not infrequently, which are like the antheridium of Marchantiales, while others are like the archegonium in their early development.

The archegonium.—The archegonia are produced from cells of the apical group and occur in an archegonial pocket. The diversities from the regular form are few; the large number of neck canal cells, the extreme development of the cap, the frequent reduction of the number of tiers of neck wall cells to five, and the somewhat massive venter may be noted. The outer cell of the two resulting from the division of the archegonial initial divides horizontally before the vertical wall is formed.

Methods of growth.—Several periods of growth may be recognized, each having a specific method of growth: the massive; the period of the cuneate apical cell extending until antheridium formation; the period of the lenticular cylindric apical cell, or the antheridial period; the period of regional apical growth, or the period of archegonium production; and the second period of massive growth, or the period of sporophyte dependence.



HUTCHINSON on PELLIA



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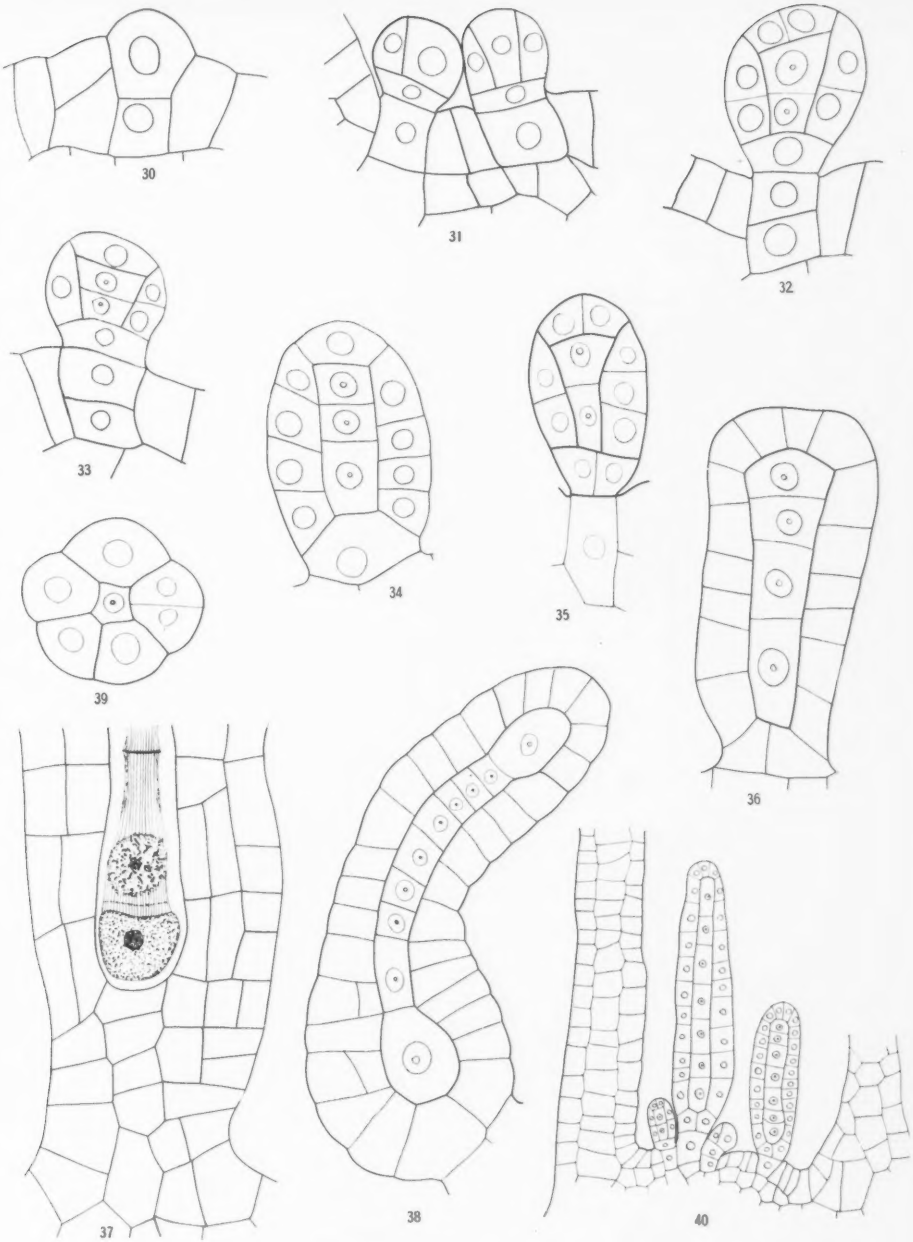

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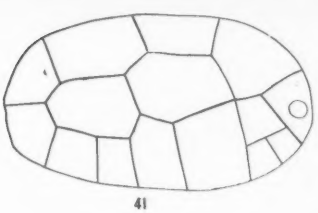
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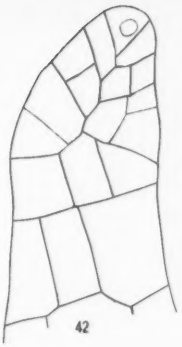
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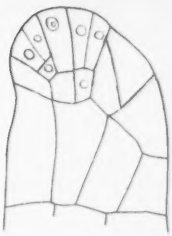
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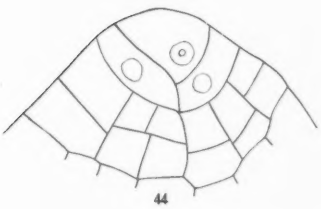
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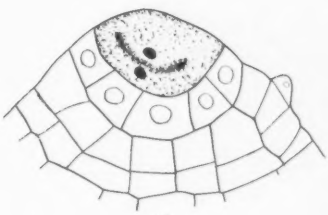
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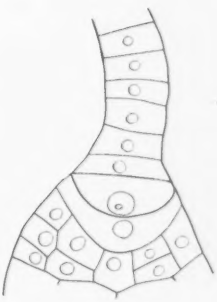
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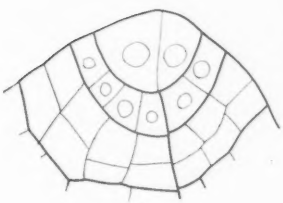
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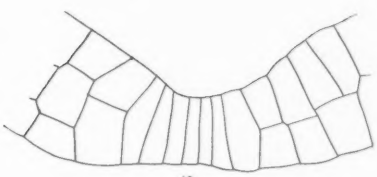
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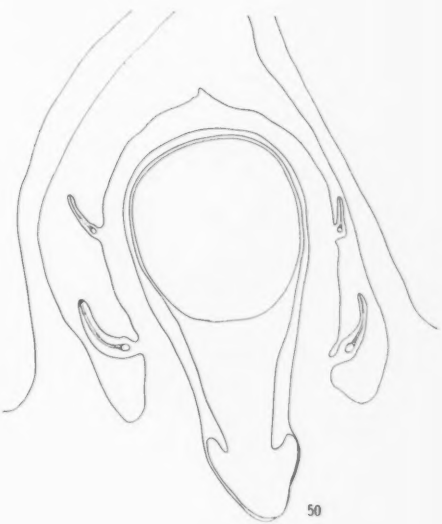
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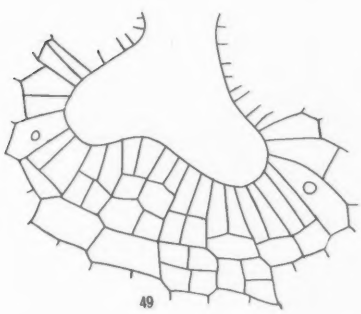
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HUTCHINSON on PELLIA

I am greatly indebted to Professor JOHN M. COULTER for suggestions and criticisms received, and to Dr. W. J. G. LAND, under whose direction the work was done.

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EXPLANATION OF PLATES I–IV

All drawings were made with the aid of the Abbé camera lucida. Original magnification of figs. 15, 40, and 50 was 500; of all other figures 1730. The reduction in reproduction is one-third.

FIGS. 1–29.—The antheridium of *Pellia epiphylla*.

FIGS. 1–6.—Longitudinal sections of a young antheridium, such as is characteristic of Jungermanniales.

FIGS. 7–9.—Cross-sections of the same.

FIGS. 10–12.—Cross-sections of antheridia of *Pellia* similar to those of *Sphaerocarpus* or Marchantiales.

FIGS. 13, 14.—Sections through the stalk (fig. 13) and spermatogenous region (fig. 14), the latter illustrating two methods of growth.

FIG. 15.—A double antheridium.

FIGS. 16–22.—Longitudinal sections of antheridia showing a development similar to that of an archegonium.

FIGS. 23–25.—Similar to last, with the elimination of the cap cell.

FIGS. 26–29.—Cross-sections of the same.

FIGS. 30–40.—The archegonium.

FIGS. 30–38.—Longitudinal sections.

FIG. 39.—Cross-section.

FIG. 40.—Cross-section of archegonial pocket.

FIGS. 41–50.—Growth structures.

FIG. 41.—A cuneate apical cell in young gametophyte which has just escaped from the spore coat.

FIGS. 42, 43.—Sections of sporeling showing the segmentation of the cuneate apical cell; fig. 42, vertical; fig. 43, horizontal section.

FIGS. 44, 45.—Transition forms of apical cells.

FIGS. 46–48.—Sections of the lenticular cylindric apical cell, also showing the region surrounding; fig. 46, a transverse vertical section; fig. 47, a longitudinal vertical section; fig. 48, a marginal longitudinal vertical section, showing how the lateral segments produce the wing or lobe.

FIG. 49.—A section through a region of apical growth.

FIG. 50.—A young sporophyte inclosed by a somewhat massive calyptra and the involucre; sterile archegonia on calyptra.

THE SCHUMANN RAYS AS AN AGENT FOR THE STERILIZATION OF LIQUIDS

W. T. Bovie

(WITH ONE FIGURE)

The early investigators were unsuccessful in their attempts to use light as a sterilizing agent, partly because of a lack of knowledge concerning the nature of the action of ultra-violet light upon living organisms, and partly because of the inefficiency of the sources of light at their command.

Finsen and his co-workers greatly extended our knowledge of the action of ultra-violet light upon living organisms, and Kuch (**6**) in 1905 (working in the laboratories of the firm of W. C. Heraeus) invented the quartz mercury vapor arc, a source of light very rich in the ultra-violet rays.

Nogier and Thevenot (**8**) in 1908 were the first to make use of the quartz mercury vapor arc in the study of the biological action of light, and Courmont and Nogier (**3**) in 1909 advocated the use of the quartz mercury vapor arc for the commercial sterilization of potable waters. They found that water which was contaminated with *Bacillus coli* and *B. Eberth* was sterilized in 1–2 minutes by a quartz mercury vapor lamp 3 dm. in length, using 9 amperes of current. The water passed through an iron tube which inclosed the quartz lamp.

In the same year Henri and Stodel (**5**) claimed to have sterilized milk with a quartz mercury vapor lamp. They performed many experiments and were certain that the milk was sterilized and that there were no bad effects on the milk such as are produced in the sterilization of milk by heat.

Courmont and Nogier (**2**) pointed out the fact that ultra-violet light does not penetrate colloidal solutions, and Dornic and Daire (**4**), in a paper on the use of ultra-violet rays for sterilization in the brewing industries, pointed out that the light could not sufficiently penetrate milk or cream to sterilize them, and that,

even if it did, the method would not be practical, because the ozone formed would be harmful to the milk and cream. They were not able to sterilize water completely by ultra-violet light, but they found that the number of bacteria was greatly reduced by the treatment.

BILLON-DAGUERRE (1), nephew of the inventor of the daguerreotype, described in 1909 a new quartz lamp for the sterilization of liquids. The source of light was a quartz discharge tube filled with rarefied hydrogen gas. Other gases were also used. Such a lamp, according to BILLON-DAGUERRE, emits Schumann rays. In a paper published in 1910 he figured an improved lamp and asserted that with this lamp water containing 29,000 bacteria (*Bacillus coli*) per cc. could be sterilized at the rate of 5 liters per minute. The discharge tube of the improved lamp was 25 cm. long and 20 mm. in internal diameter. It was excited by the current from the secondary of an induction coil which gave a spark 15 mm. in length; the primary of the induction coil was operated by a current of 2 amperes at 6 volts. He said that the lamp was more than 20 times as efficient as the mercury vapor arc.

URBAM, SCAL, and FEIGE (9) questioned the efficiency of Schumann rays for sterilizing, because of their small penetrating power. They recommended a lamp with terminals of carbon and of aluminum for sterilizing large quantities of water.

LYMAN (7) studied the absorption by water of the Schumann rays and showed that light of wave-length 1750 Ångström units was completely absorbed by a layer of water 0.5 mm. thick. He pointed out the improbability of the results claimed by BILLON-DAGUERRE.

The Schumann rays are undoubtedly very active chemically, but they have such a small penetrating power that it seemed improbable to Professor LYMAN (at whose suggestion the writer undertook this work) that in a sterilizer such as described by BILLON-DAGUERRE the bacteria would be exposed to sufficient light to kill them. BILLON-DAGUERRE passed the water, which he was attempting to sterilize, through his apparatus at so rapid a rate that sufficient exposure for sterilization seems impossible, since the organisms in the water could be affected

by the rays only during the times when they were in very close proximity to the discharge tube.

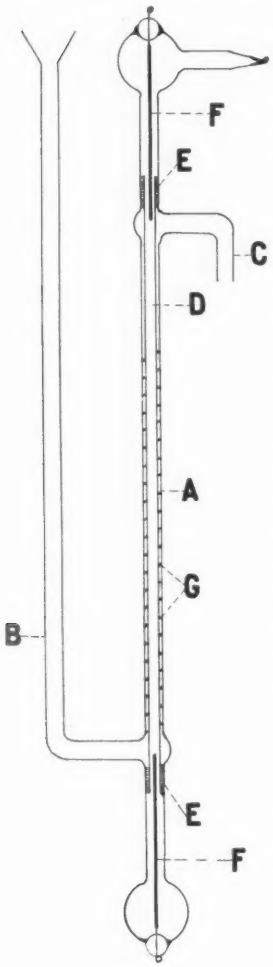

FIG. 1

In order to test the efficiency of BILLON-DAGUERRE'S method, a sterilizer similar to the one which he described was constructed by the writer, and distilled water, contaminated with various bacteria, was passed through it. Although the water passed through at a much slower rate than the one given by BILLON-DAGUERRE, the water was not sterilized. Another sterilizer was then constructed in which the organisms could receive a much longer exposure; the discharge tube was longer, the volume of liquid exposed at any one time was much less, and the chance of the bacteria coming in close contact with the discharge tube was much greater, as the liquid was caused to circulate around the discharge tube. The construction of the improved sterilizer is shown in fig. 1. A glass tube *A* with bulbs on each end, into which electrodes *F* were sealed, had side tubes as shown at *B* and *C*. The electrodes were of aluminum. The tube *B* served as the inlet and *C* as the outlet for the liquid under treatment. Within the glass tube there was a very thin-walled tube of quartz (*D*). The distance between the outside of the quartz tube and the inside of the glass tube was 0.3 mm. The quartz tube was sealed to the glass tube at *E*, *E* with DeKotinski cement, so that the space between the two tubes was not in communication with the remainder of the interior of the

glass tube. A gold wire was drawn down exactly to fit this space. The wire was coiled spirally around the quartz tube as shown at *G*. The distance between the inlet tube *B* and the outlet tube *C* was 16 cm. The quartz tube was 5 mm. in outside diameter, and the gold wire made 15 turns about the quartz tube. The solution under treatment was thus spread into a thin layer, 0.3 mm. in thickness, and took a spiral course through the sterilizer. The discharge tube was filled with rarefied unwashed hydrogen, containing carbon dioxide as an impurity, since a discharge tube filled with pure hydrogen would not emit light of wave-lengths between 2000 and 1675 Ångström units. The carbon dioxide which the tube contained filled in this gap. This is important, for it is highly improbable that the strong 1600 lines of the hydrogen spectrum, because of their small penetrating power, could be effective in sterilizing the water. Any virtue which the sterilizer might have must be due to its emitting light between wave-lengths in 1850 and 1675 Ångström units.

A discharge tube filled with carbon dioxide is short-lived. After the tube has been excited a few hours, the carbon dioxide disappears and is replaced by hydrogen. To insure a carbon dioxide spectrum, the discharge tube was filled and pumped before each experiment.

The discharge tube was excited by a current of 14 milliamperes, and Cambridge city water was passed through the sterilizer at the rate of 10 cc. per minute. By this treatment the bacterial count of the water was reduced from 50 to 4 per cc., and the fungal count from 3 to 1 per cc. In none of the experiments was the water completely sterilized.

It is apparent that a hydrogen discharge tube such as is described by BILLON-DAGUERRE is not an efficient source of light for photo-sterilization.

LABORATORY OF PLANT PHYSIOLOGY
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SOME FILAMENTOUS FUNGI TESTED FOR CELLULOSE DESTROYING POWER[1]

FREEMAN M. SCALES

Every year large quantities of cellulose in the various combinations occurring in plant tissue are returned to the soil. In this tissue there is also a great deal of carbohydrate material, such as sugar, starch, pectose, and hemicellulose. These substances are more easily available and will under ordinary circumstances be all used up before the cellulose is attacked. In spite of this abundance of easily available food, at the end of several months practically all the plant tissue will be disintegrated and split into soluble substances and humus. The destruction of this large quantity of cellulose in such a comparatively short time means that the cellulose destroying organisms must work very vigorously. By special methods of culture, cellulose dissolving bacteria have been obtained which hydrolyze this complex material very rapidly, but when plating on cellulose agar directly from a soil for the isolation of cellulose destroying organisms the filamentous fungi usually grow more abundantly and destroy more cellulose than do the bacteria. In order to determine whether the addition of cellulose to soil makes any difference in the number of molds in it, 2 per cent of cellulose was added to 200 grams of soil which was moistened to the optimum with distilled water and then incubated for 30 days at 30° C. The initial count of this soil on cellulose agar was 20,000 mold colonies. A check sample which received no cellulose, but otherwise had the same treatment as the one described, gave on the same kind of media a count of 100,000 mold colonies, while the sample which received cellulose showed a mold content of 200,000,000. It is evident from these data that the filamentous fungi are an important factor in the dissolving of cellulose in the soil.[6]

It is a well known fact that filamentous fungi are very numerous in woodland soils and also that they are abundant in acid arable

[1] Published by permission of the Secretary of Agriculture.

soils where the reaction is naturally favorable for them. MARCHAL[2] found numerous mycelia of molds in acid humus soils which were naturally rich in organic material, and he believed that they took an active part in the mineralization of organic nitrogen under these conditions, but that in an arable soil under active cultivation the molds were relatively few in number owing to the alkaline reaction and the absence of large quantities of organic matter. While the filamentous fungi are naturally thought of as occurring in great numbers in acid soils, still the recent work of DALE[3] in England indicates that in some cultivated alkaline soils they are just as numerous. JENSEN[4] at Ithaca found a great variety of filamentous fungi in alkaline cultivated soils. Lately TRAAEN[5] has reported the results of his investigation of the species and physiological activity of some of the soil fungi of Norway. In our own investigations on the destruction of cellulose by bacteria and filamentous fungi, we worked almost entirely with alkaline soil that had been under active cultivation, and found among the fungi occurring in both great variety and enormous numbers many species active cellulose destroyers. The physiological activities of these organisms on organic material, whether nitrogenous or not, are well recognized. All these data indicate that the filamentous fungi are important factors in carrying on the biological processes in cultivated soils.

In further study[6] of the destruction of cellulose by microorganisms, 19 species of cellulose destroying filamentous fungi were identified and two new ones found. One of these species was found[7] to produce a very active cytase. The present work was

[2] MARCHAL, EMILE, Sur la production de l'ammoniaque dans le sol par les microbes. Bull. Acad. Roy. Belgique III. **25**:741. 1893.

[3] DALE, ELIZABETH, On the fungi of the soil. Ann. Mycol. **10**:452–477. *pls. 5.* 1912; **12**:33–62. *pls. 5.* 1914.

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[6] MCBETH, I. G., and SCALES, F. M., The destruction of cellulose by bacteria and filamentous fungi. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 266. 1913.

[7] KELLERMAN, K. F., Formation of cytase by *Penicillium pinophilum*. Bur. Pl. Ind. Circ. no. 113. pp. 29–31. 1912.

undertaken for the purpose of determining more species of the filamentous fungi that are capable of exercising this function.

Dr. CHARLES THOM, mycologist of the Bureau of Chemistry, kindly supplied us with the 30 species of *Penicillium* and 10 species of *Aspergillus* that were used in this work. The cellulose destroying power of these organisms was determined with two different sources of nitrogen. An ammonium sulphate cellulose agar and a peptone cellulose agar were used for this purpose. The ammonium sulphate medium was prepared by the method described in a previous publication,[6] and the peptone medium by substituting 1 gram per liter of peptone for the ammonium sulphate.

The stock cultures were kept on Czapek's agar. The spores from fresh growths on this medium were added to freshly poured duplicate cellulose agar plates of both media. The plate cultures were inoculated in four places. Test tube cultures on both media were also made in duplicate at the same time. The Petri dishes were placed in moist chambers and then put in the incubator along with the tube cultures, which were kept at 28–30° C. for two months. They were then examined for an enzymic zone either around the colony on the plates or underneath it in the tubes. The size of this enzymic area varied considerably in the different cultures, ranging from a very thin clear zone less than 1 mm. to one 24 mm. deep in some of the tubes. Although the depth of the clear zone was fairly constant in the duplicate tubes, this phase of the work will not be emphasized until more data are obtained.

As the surface growth on cellulose agar is frequently scanty, with few definite microscopic differences, it seemed best to transplant from the plates and tubes onto Czapek's agar, in order to check each organism that destroyed cellulose against a growth on Czapek's agar made from the stock material of this species. A microscopic examination was made in each case.

The results are given in the accompanying table. The apparent failure of a number of the organisms fermenting cellulose with ammonium sulphate as the source of nitrogen to do the same with peptone as the source of nitrogen may be accounted for in two ways. One is that the organisms produced such an abundant sterile growth in the medium that any slight clearing was obscured;

the other is that the carbon in the peptone was utilized, being more easily available, and the cellulose was not attacked.

TABLE I

RESULTS OF THE TEST TO DETERMINE THE CELLULOSE DESTROYING POWER OF SOME FUNGI WITH DIFFERENT SOURCES OF NITROGEN

+ indicates cellulose destroyed; − indicates cellulose not destroyed.

	Species	Ammonium sulphate	Peptone
1*a*.	Penicillium luteum Zukal	+	+
2*a*.	" pinophilum Hedg.	+	−
3*a*.	" rugulosum Thom	+	+
4*a*.	" sp. no. 2670 Thom.	+	−
5*a*.	" purpurogenum O. Stoll.	+	+
6*a*.	" duclauxi Dela.	+	.....
7*b*.	" commune Thom.	−	−
8*b*.	" biforme Thom	−	−
9*b*.	" sp. no. 66 Thom.	−	−
10*b*.	" sp. no. 13 Thom.	+	+
11*c*.	" expansum Link	+	+
12*c*.	" sp. no. 2694 Thom	+	−
13*d*.	" chrysogenum Thom.	+	+
14*d*.	" notatum West	+	.....
15*d*.	" sp. no. 12 Thom	+	.....
16*e*.	" camemberti Thom.	−	−
17*e*.	" camemberti var. rogeri Thom	−	−
18*f*.	" intricatum Thom.	+	+
19*f*.	Spicaria simplisissima Jensen	+	−
20.	Penicillium lanosum West.	+	+
21.	" claviforme Bainier.	+	+
22.	" granulatum Bainier.	+	+
23.	" roqueforti Thom.	+	+
24.	" spinulosum Thom	+	−
25.	" funiculosum Thom	+	.....
26.	" lilacinum Thom	−	−
27.	" divaricatum Thom	−	−
28.	" sp. no. 64 Thom.	+	+
29.	" sp. no. 3505 Thom.	+	−
30.	Scopulariopsis repens Bainier.	+	−
31.	Aspergillus candidus Link	−	−
32.	" clavatus Desm.	+	−
33.	" flavus Link	+	+
34.	" fumigatus Fresen.	+	+
35.	" nidulans Eidam	+	−
36.	" niger VanTiegh	+	+
37.	" oryzae Ahlb	+	−
38.	" Wentii Wehmer	+	−
39.	" sp. no. 144 Thom*	+	+

*Another culture of this species sent in from the Riverside Experiment Station, California, by Mr. I. G. McBETH, gave the same reactions.

Some cultures of *Actinomyces* that have been accumulated for a classification of this group were also tested, and of 31 cultures, 8

dissolved the cellulose agar containing ammonium sulphate as a source of nitrogen. These cultures all show marked microscopic differences and are without doubt different species. These 8 organisms may be of the same species as some of the 12 cellulose destroying species which KRAINSKY[8] has recently described.

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[8] KRAINSKY, A., Die Aktinomyceten und ihre Bedeutung in der Natur. Centralbl. Bakt. **41**:649–688. 1914.

BRIEFER ARTICLES

THE RELATIVE IMPORTANCE OF DIFFERENT SPECIES IN A MOUNTAIN GRASSLAND

A careful study has been made by the writer through four seasons upon an area of dry grassland in a mountain park at Tolland, Colorado. The park (altitude 8889 feet) is a widened area in the valley of South Boulder Creek. The dry grassland covers most of those parts of the park that lie from 10 to 50 feet above the stream level.

As a part of the investigation 16 quadrats, each a meter square, were staked off and examined from time to time through the four seasons of study. Most of these quadrats are on morainic material, but a few are on the upper creek terraces. In the quadrats 64 species of plants were found, while the entire dry grassland area of the park showed 62 species in addition.

Estimates were made, as explained in a former paper,[1] of the amount of bare ground in each quadrat and also the area covered by each species of plant. By combining the figures for the different quadrats, the relative abundance of the various plants was determined. While the figures for the less frequent species are of little value, those for species occurring in any considerable number of quadrats show well the relation of these plants to the composition of the association as a whole. It is certain that every plant of frequent occurrence in the dry grassland of the park is represented in a number of quadrats.

The data for July 1913 are gathered together in table I. These midsummer records have been selected for presentation as probably of greater interest than would be the figures for spring or autumn. In certain genera two or more species of similar ecological nature have been put together as one item, the names arranged in order of importance.

According to the records, the two species present in the quadrats in greatest abundance are *Artemisia frigida* and *Aragallus Lambertii*, but *Muhlenbergia gracilis* and *Carex stenophylla* are almost equally important. Plants of the different species of *Carex* taken together cover a larger part of the area than do those of any single grass genus, but the grasses as a whole are of much greater importance than the sedges. The most abundant grasses are the species of *Muhlenbergia*,

[1] Bot. Gaz. **57**:526–528. 1914.

TABLE I

PERCENTAGE COMPOSITION OF THE DIFFERENT QUADRATS, JULY 1913

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XIIa	XIII	XIV	XV	XVI	Total	Percentage of ground covered	Percentage of total vegetation
Bare ground	30	33	50	13	20	28	20	45	20	10	15	15	20	25	25	30	399	24.94	.....
Small gray lichen	...	...	...	1	...	1	...	...	...	5	1	...	...	...	...	2	10	0.63	0.84
Selaginella densa	...	...	...	5	...	3	20	10	...	5	5	...	15	...	5	1	69	4.31	5.75
Agropyron violaceum	2	...	2	8	10	...	...	...	2	3	...	2	...	2	10	...	41	2.56	3.41
Agrostis hiemalis	2	...	...	...	...	...	...	...	...	...	...	...	...	...	...	...	2	0.13	0.17
Avena americana	...	...	1	...	...	...	...	...	...	5	...	...	10	...	...	...	16	1.00	1.33
Blepharineuron tricholepis	...	...	...	...	...	...	...	...	...	...	...	2	...	...	...	...	2	0.13	0.17
Bromus Pumpellianus	...	...	...	...	1	5	...	1	...	...	...	...	...	...	...	...	7	0.44	0.59
Danthonia Parryi and intermedia	...	...	...	...	...	...	...	...	...	2	5	...	...	...	10	4	21	1.31	1.75
Festuca ingrata, saximontana, rubra	5	...	...	5	12	15	19	...	...	10	...	26	...	...	...	...	92	5.75	7.67
Koeleria cristata	2	...	...	5	10	5	...	1	...	...	5	5	...	2	...	3	38	2.38	3.17
Muhlenbergia gracilis and subalpina	...	...	15	19	12	...	...	...	15	...	10	...	25	...	...	1	97	6.06	8.08
Poa interior, crocata, rupicola, subpurpurea	3	...	3	5	5	3	...	...	2	10	...	15	...	...	2	5	53	3.31	4.41
Sitanion elymoides	...	...	...	...	...	...	...	...	1	...	4	...	...	...	...	...	5	0.31	0.41
Stipa comata, minor, Nelsoni	...	...	...	...	2	...	...	...	29	...	1	...	...	...	...	...	32	2.00	2.66
Carex filifolia	...	...	...	...	...	...	...	...	...	5	20	...	...	...	16	...	41	2.56	3.41
Carex stenophylla and pennsylvanica	2	25	4	...	3	...	1	21	2	...	...	...	...	20	2	20	100	6.25	8.33
Juncus balticus	...	...	...	2	...	5	...	...	...	5	2	2	2	1	2	1	22	1.38	1.84
Allium recurvatum	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	...	1	0.06	0.08
Comandra pallida	...	...	...	...	3	...	...	...	5	...	2	...	...	...	2	...	12	0.75	1.00
Eriogonum umbellatum	...	...	...	...	5	...	...	...	10	...	5	...	...	...	...	...	20	1.25	1.67
Arenaria Fendleri	...	...	...	1	...	1	...	1	...	...	...	...	1	1	1	2	8	0.50	0.66
Cerastium occidentale	...	...	2	...	1	1	...	...	2	5	3	9	2	1	5	...	31	1.94	2.58
Silene Hallii	...	...	...	3	...	...	...	...	...	...	1	...	...	...	...	...	4	0.25	0.33
Erysimum Wheeleri	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1	0.06	0.08
Sedum stenopetalum	...	2	2	1	3	1	...	1	3	...	2	2	2	1	5	...	25	1.56	2.08
Saxifraga rhomboidea	...	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	1	0.06	0.08

TABLE I—*Continued*

	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	Total	Percentage of ground covered	Percentage of total vegetation
Potentilla pennsylvanica strigosa, concinna	1	2	...	1	...	...	...	1	1	...	...	...	...	11	...	...	17	1.06	1.41
Potentilla Hippiana, gracilis, Nuttallii	2	2	...	...	...	10	2	...	...	...	...	...	5	...	...	...	21	1.31	1.74
Aragallus deflexa	17	...	...	2	...	...	...	...	...	...	...	...	...	...	...	...	19	1.19	1.58
Aragallus Lambertii	...	5	...	12	5	2	...	10	...	10	5	...	5	20	5	...	79	4.94	6.58
Aragallus Richardsonii	20	...	...	4	...	...	...	...	1	...	...	...	...	10	...	2	37	2.31	3.08
Astragalus Parryi	...	...	...	...	...	...	...	...	1	...	...	...	...	...	...	...	1	0.06	0.08
Pseudocymopterus tenuifolius	...	...	...	...	...	...	1	...	...	...	...	1	1	...	...	...	3	0.19	0.25
Vaccinium caespitosum	...	...	...	...	...	...	20	...	...	...	...	...	...	...	...	...	20	1.25	1.66
Androsace puberulenta	...	...	...	...	...	...	...	...	...	...	...	...	...	...	1	...	1	0.06	0.08
Gentiana Parryi	...	...	...	1	...	...	3	...	...	...	...	...	...	...	...	...	4	0.25	0.33
Mertensia Bakeri	...	...	5	2	1	2	2	...	...	...	2	5	2	2	2	1	26	1.62	2.16
Orthocarpus luteus	...	...	...	2	...	...	...	...	...	5	...	1	...	...	...	10	18	1.12	1.49
Pentstemon procerus	...	...	...	...	...	...	3	...	...	...	...	2	...	...	...	...	5	0.31	0.41
Campanula petiolata	...	...	...	...	1	...	2	...	...	5	2	2	...	...	...	...	12	0.75	1.00
Achillaea lanulosa	...	...	5	...	...	...	2	...	1	...	...	5	3	...	...	...	16	1.00	1.33
Antennaria aprica	...	...	...	...	...	...	...	...	...	5	...	...	...	...	...	...	5	0.31	0.41
Artemisia aromatica	1	5	1	1	1	...	...	...	...	...	...	...	...	...	3	4	16	1.00	1.33
Artemisia frigida	10	25	5	5	5	5	1	...	5	5	10	2	5	2	...	5	90	5.62	7.49
Chrysopsis foliosa	1	...	3	...	...	8	4	...	...	5	...	2	1	...	3	1	28	1.75	2.33
Erigeron formosissimus	...	...	...	...	...	...	...	...	...	...	...	1	...	...	...	...	1	0.06	0.08
Erigeron trifidus	2	1	...	...	...	...	...	8	...	...	...	...	...	2	...	...	13	0.81	1.08
Gaillardia aristata	...	...	...	2	...	...	...	...	...	...	...	...	...	...	...	8	10	0.63	0.84
Solidago decumbens	...	...	...	...	...	5	...	...	...	...	...	...	...	...	...	...	5	0.31	0.41
Troximon glaucum	...	...	2	...	...	...	...	...	...	...	...	1	...	...	...	...	3	0.18	0.24
Total	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	1600	99.97	99.94

followed in order by the species of *Festuca*, *Poa*, *Agropyron*, *Koeleria*, and *Stipa*. If the dry grassland were to be named by its chief generic constituents, it would be called a *Carex-Artemisia-Aragallus-Muhlenbergia* association.

From table II it will be seen that in the midsummer of 1913 two-

TABLE II

THE CHIEF CONSTITUENTS OF THE VEGETATION OF THE QUADRATS

Names of plants	Percentage of ground covered	Percentage of vegetation
Selaginella densa	4.31	5.75
Agropyron violaceum	2.56	3.41
Festuca ingrata, saximontana, rubra	5.75	7.67
Koeleria cristata	2.38	3.17
Muhlenbergia gracilis and subalpina	6.06	8.08
Poa crocata, interior, rupicola, subpurpurea	3.31	4.41
Stipa comata, minor, Nelsoni	2.00	2.66
Carex filifolia	2.56	3.41
Carex stenophylla and pennsylvanica	6.25	8.33
Cerastium occidentale	1.94	2.58
Aragallus Lambertii	4.94	6.58
Aragallus Richardsonii	2.31	3.08
Artemisia frigida	5.62	7.49
Total	49.99	66.62

TABLE III

THE MOST IMPORTANT PLANT FAMILIES AND THEIR PART IN THE VEGETATION OF THE QUADRATS

Names of families	Percentage of ground covered	Percentage of vegetation
Poaceae (19 species)	25.38	33.82
Carduaceae (10 species)	11.49	15.30
Cyperaceae (3 species)	8.81	11.74
Fabaceae (4 species)	8.50	11.32
Selaginellaceae (1 species)	4.31	5.75
Total	58.49	77.93

thirds of the vegetation of the quadrats was made up of plants listed in 13 items in the first table. A certain few plants that are widely distributed do not make up a large percentage of the ground cover and are therefore not listed in table II. The most important of these are *Juncus balticus*, *Arenaria Fendleri*, *Sedum stenopetalum*, *Mertensia Bakeri*, and *Chrysopsis foliosa*, each of which was found in 9 or more of the quadrats.

The five plant families best represented in the quadrats are shown in table III.—FRANCIS RAMALEY, *University of Colorado, Boulder, Colo.*

CURRENT LITERATURE

BOOK REVIEWS

Plant poisons and stimulants

The first volume of the Cambridge *Agricultural monographs*[1] covers a very much more restricted field than the title would lead one to expect, since it deals only with the effects, mainly upon the higher plants, of compounds of the five elements, copper, zinc, arsenic, boron, and manganese. Miss BRENCHLEY has previously published some of the results of work with these compounds which she has been carrying on since 1907 at the Rothamstead Experimental Station,[2, 3] these results being here brought together in connection with a résumé of certain portions of the related literature.

An introductory chapter of six pages points out that the classification of the elements into the three groups, nutritive, toxic, or indifferent as respects their action upon plants, no longer holds, and expresses the belief that no such simple grouping is possible. The second chapter describes the water culture methods employed by the author in her work, discusses the comparative advantages and disadvantages of water, sand, pot, and field experiments, emphasizes the necessity for caution in comparing results obtained by these different methods, and asserts that "all crucial experiments have always been and must always be done in water cultures." Then follow five chapters, each devoted to discussion of the physiological effects of compounds of one of the five elements employed. The subdivisions of these chapters deal with such topics as the occurrence of the element in higher plants, its effects upon growth when present alone in water cultures, when present along with nutrient or non-nutrient salts or with insoluble substances, its effects upon growth in soils, its action upon algae and fungi, and its effects upon germination of seeds and spores. A four-page chapter entitled "Conclusions" and a bibliography of 182 titles complete the work.

The general conclusions reached are that compounds of copper, arsenic, and in all probability those of zinc also, do not exert stimulatory effects in any concentration when added to water cultures of higher plants, but are toxic at all concentrations having a discoverable effect. A stimulatory effect of each of

[1] BRENCHLEY, WINIFRED M., Inorganic plant poisons and stimulants. 8vo. pp. 110. *figs. 19.* Cambridge: University Press. 1914.

[2] BRENCHLEY, WINIFRED M., The influence of copper sulphate and manganese sulphate upon the growth of barley. Ann. Botany **24**:571–583. *pl. 47.* 1910.

[3] ———, On the action of certain compounds of zinc, arsenic, and boron on the growth of plants. Ann. Botany **28**:283–301. 1914.

these salts for such fungi as *Aspergillus* and *Penicillium*, and in the case of zinc, for the lower algae also, is definitely shown by the literature. Boron and manganese compounds in low concentration are stimulatory for higher plants; peas show stimulation by boric acid to a greater degree, by manganese to a less degree, than does barley. *Aspergillus*, *Saccharomyces*, and green algae are indifferent to high concentrations of boric acid, while there is no evidence in the literature that it is stimulatory at any concentration. The contradictory results obtained by RICHARDS and LOEW and SAWA as respects the effects of manganese upon fungi are reviewed, but no opinion is expressed.

The introductory chapter states that "a voluminous literature has arisen around the subject, and in the present discussion some selection has been made with a view to presenting ascertained facts as succinctly as possible. No attempt has been made to notice all the papers; many have been omitted perforce; it would have been impossible to deal with the matter within reasonable limits otherwise." A successful attempt of this sort requires that one have at least as great familiarity with what is left out as with what is included. But it must be said that Miss BRENCHLEY has not this knowledge, and that the character and importance of the omitted literature is such as to make the book very far from "a succinct presentation of the ascertained facts." For while the various chapters include discussions of the effects upon the fungi and the algae of the five elements under discussion, the citations made betray unfamiliarity with the literature; not only do they fail to give any idea of the enormous extent of the work done in this field, but they are by no means those which add most, either to the body of observed facts or to our present conceptions of the nature and effects of salt action upon lower forms. To cite important omissions would be to fill pages of this journal, and an example or two must suffice to illustrate a general situation. Thus, there is nowhere in the several sections dealing with change of form in algae and fungi when grown in salt solutions any mention of osmotic pressure as a significant factor; indeed the words do not occur in the book, and there is no reference to the work of KLEBS, LIVINGSTON, and the host of others who have furnished our present knowledge of this phase of the subject. Again, while the effects of copper sprays upon foliage, a subject which has long received particular attention at the hands of American physiologists and pathologists, is discussed to the extent of three pages, no American worker finds a place among the seven whose work is cited, and the most recent paper mentioned appeared in 1908. Such omissions would be surprising in any case; they become inexcusable when we recall that the very recent paper of PICKERING and the DUKE OF BEDFORD, certainly readily accessible to any English worker, not only furnished important results of work done at the Woburn Fruit Farms, but also admirably summarized the results of others up to the time of its publication. That the author reaches conclusions as to the effects of Bordeaux mixture upon assimilation and transpiration which are diametrically opposed to those of most recent workers, as for example REED and DUGGAR, is therefore not surprising. All the sections

dealing with the action of salts upon the lower plants are of this character, not only failing wholly to present the literature adequately, but making such bizarre selections therefrom as to force the conclusion that the papers discussed were brought together, like Cain's rejected sacrifice, "unculled, of such as came to hand." It is sincerely to be regretted that these sections of the book were not submitted to some physiologist or pathologist whose acquaintance with this field might have made of them a reliable summary of our present knowledge.

If those portions of the book which are concerned with higher plants had been intended simply as a compilation of results of authors who have recorded visible effects of salts on plants, they would have fallen short of the mark by reason of the many and important omissions both of American and of German work. But the work professes to be critical, and this it emphatically is not. The author nowhere gives expression to her own beliefs or convictions in clear, unmistakable terms, nor does she evaluate for us the ideas of others. Conclusions of the earlier workers, filled as they are with mistaken interpretations of results, are repeated without comment, and unproven assumptions and exploded theories stand side by side with established fact. Consequently, the reader not already thoroughly familiar with the literature will at once lose his bearings and grope his way blindly through a maze out of which he will carry at least as much of fundamental error as of "ascertained facts."

But it is in the sections dealing with the mode of action of toxic compounds upon protoplasm that the book is most vitally defective. The last ten years have been years of extraordinary advance in the study of protoplasmic permeability and of its modifications under the action of external agencies, and the facts gained in this field have been utilized by a host of workers in formulating theories of toxic and antitoxic action as phenomena arising primarily from modification of permeability. The literature dealing with these subjects is readily accessible and has, moreover, recently been summarized in new editions of CZAPEK's *Biochemie* and HOEBER's *Physikalische Chemie;* consequently there are few American physiological laboratories in which the new knowledge has failed to find its way into undergraduate instruction. Consequently it is amazing to find that the author of the book under review has nowhere mentioned any portion of this literature; that LEPESCHKIN, TRÖNDLE, CZAPEK, HOEBER, and RUHLAND are not mentioned; that the conceptions of salt action which we owe to WOLFGANG OSTWALD, MOROWITZ, FLURI, SZÜCS, PAULI, DERUFZ DE LAVISON, and HANSTEEN CRANNER, with a host of others, nowhere appear, and that the author's ideas of the whole subject are of the character generally held before 1900, when the ion-proteid theory of PAULI and LOEB appeared. A few examples will suffice to indicate this. The discussion of the nature of stimulation confounds increased permeability to water and consequent increase in green weight with true stimulation of protoplasmic activity, as on pp. 2, 3, 75, and this confusion exists throughout. One reads (pp. 40–41) that "it is very striking to see the desperate efforts that badly

poisoned pea plants make to reproduce themselves. . . . . In the greater strengths of such poisons as zinc and copper sulphate [*sic*] root growth is checked from the outset, but usually a very little shoot growth is made, and one frequently obtains ridiculous little plants about an inch high bearing unhappy and diminutive flowers, which are occasionally replaced [succeeded is meant] by equally unhappy and miniature fruits." The author fails to apprehend that the source and fount of all this woe is a lowered permeability for water, with a resultant development in which lack of water is the limiting factor. This is also the case with the plants of *Pisum*, *Phaseolus*, and *Zea* described on p. 18; the high concentration of copper sulphate here employed totally inhibited root development, but the resultant strong growth of tops, instead of being due to "stimulation of the shoots by some physiological process or other," as the author thinks, is exactly what we find wherever inhibition of root development, however caused, permits the utilization of the foodstuffs present in the seed solely in the development of aerial parts. The most remarkable passage in the book, however, is undoubtedly that on p. 27, in which we are told that "so long as the solution of copper salts is dilute enough, the absorption layer of the root, acting as a semipermeable membrane and upheld by the resistant protoplasm, is able to keep the copper out of the plant and to check its toxicity. As soon as a certain limit is reached the copper exercises a corrosive influence upon the outer layer of the root whereby its functions are impaired, so that it is no longer able efficiently to resist the entry of the poison. As the concentration increases it is easy to conceive that the harmful action should extend to the protoplasm itself." Just what this "absorption layer" may be the author does not tell us; it seems not to be protoplasmic, and inasmuch as it seems to combine the active rôle of Horatius at the bridge with the more passive function of the Holland dikes, physiologists will regret that we are told no more of its origin, functions, and relation to cell wall and protoplasm than has been quoted.

That the book is exceedingly disappointing will be obvious from these quotations. Physiologists have been awaiting the appearance of a résumé of the whole subject of toxic action which would bring together the extensive observations of the older literature and unify and explain them in the light of the new knowledge of the nature and behavior of the protoplasmic membrane. The author who successfully undertakes the task must have kept abreast of the literature in many fields; with the tremendous advances made in physical chemistry and in our knowledge of the colloids, no less than with the work done directly with the subject in hand, for most help will come from the literature of these related fields. It is just here that Miss BRENCHLEY has failed; her book merely collects a mass of observations which it will be the task of some future physiologist possessing wide training and a modern point of view to organize and explain.

There are various minor omissions and slips of the pen. Thus while formulae for two nutrient solutions are given on p. 13, we are nowhere told,

in the various sections dealing with experiments in which plants in nutrient solutions were employed, which of these was used in any particular case. The description of HASELHOFF's experiments (p. 25) leaves the reader to wonder whether each sample of soil was extracted with 375 liters of water, divided into 15 equal quantities, or with 25 liters used 15 successive times. The substitution of "below" for "above" in line 8, p. 30, would lead the unwary reader to conclude that the toxicity of copper is decreased as the concentration of the solution increases. The citations of literature are not numbered, and when a given author has a number of papers listed in the bibliography, the reader has no means of knowing what particular citation contains the results quoted in the text. While physiologists have universally adopted the terminology of the normal solution, concentrations are here written as parts per thousand or million, and when quotations from authors who follow the modern custom are made, normal solutions are sometimes converted to parts per million, sometimes have equivalents parenthetically introduced, and are sometimes carried over unchanged. Consequently, comparison of the figures is impossible without resorting to calculation. In the graphs showing dry weight of plants grown in various concentrations of salts, some one concentration, as 1/100,000, is chosen as a "unit," and other concentrations are written in the graph as multiples or fractions of this unit, making easy reference impossible. Those hyphenated and immortal acquaintances of our early youth, "carbo-hydrate" and "photo-synthesis," greet a surprised public in these pages once more, after a generation of absence from the ken of physiologists.

The concluding paragraph gives naïve expression to a point of view which physiologists had supposed to be happily confined to a certain rapidly decreasing class of agricultural workers in this country. After discussing the results obtained by physiological experimentation with manganese and boric acid and those obtained in field trials of stimulatory fertilizers, the author says, "the possibility now exists that in some respects the two lines of work are converging and that the more purely scientific line will have a big contribution to make to the strictly practical line." Those of us who regard plant physiology as the science of economic plant production had thought that the artificial lines of demarcation between "scientific" and "practical" work had long ago disappeared, and that future progress was to be made, not independently or along convergent lines, but by the common utilization of scientific facts and methods in the cooperative attack upon common problems. In view of the fact that the long series of publications from the Rothamstead Experimental Station have set a standard to which comparatively little of the agricultural literature of this country has attained, it is surprising that this book, with its lamentable deficiencies in grasp of subject-matter and in point of view, should have been issued as the initial number of a series of monographs whose general editors are Professor WOOD, of Cambridge, and Director RUSSELL, of Rothamstead. Closer editorial supervision would have withheld the book from publication

in its present form, and it is to be hoped that immediate and radical revision may make of it an acceptable and trustworthy guide to the literature of this interesting field.—JOSEPH S. CALDWELL.

NOTES FOR STUDENTS

Experimental embryology.—Morphologists and experimental workers have been aware for some time of a need of greater cooperation between their respective lines of research. Too often morphological or cytological studies are pursued without reference to important physiological conditions, while conclusions are drawn from experimental work which would not be warranted by morphology and cytology. It is becoming increasingly evident that results can be more properly interpreted in the additional light afforded by supplementary researches in a related field. The value of this cooperative method is emphasized in a recent paper by KUSANO[4] on angiosperm embryology. A favorable form for such study was found in the orchid *Gastrodia elata*. Since the inflorescence develops at the expense of material stored in a tuber, it is a simple matter to maintain the plant under normal nutritive conditions. Some of the results of KUSANO'S research, which is still in progress, are cited below.

The normal development in *Gastrodia* is as follows: A subepidermal archesporial cell becomes the megaspore mother cell and undergoes the two maturation divisions. In some cases reduction, which is said to consist in a simple pairing and separation of the chromosomes on the equator of the spindle, fails to occur, so that the functioning megaspore and gametophyte are sometimes haploid and sometimes diploid. The embryo sac contains only 4 nuclei, 3 of which are organized as an egg apparatus. This reduced condition is regarded as an economical specialization correlated with the peculiar vegetative habit. Many irregularities which occur are related to poor nutrition. At fertilization, which occurs only in haploid sacs, one of the male nuclei fuses with the egg nucleus, while the other fuses with the single polar and a synergid nucleus. The fertilized egg forms the usual undifferentiated proembryo, which is nourished through the suspensor and large nucellar cells. The endosperm nucleus does not divide. The following time schedule was determined: two days before the flower opens the ovule is yet in a rudimentary stage; the embryo sac is completed 3 days after bloom; fertilization occurs the 4th day after pollination; the fertilized egg divides the 5th day; the seed is completed the 14th or 15th day; the capsule dehisces about the 23d day. This exceptionally rapid development (for Orchidaceae) is correlated with the fact that it occurs at the expense of stored food. Occasionally two archesporial cells arise in a single ovule and undergo complete development.

An extended series of experiments led to the following conclusions: After a few days the fertilizing power of the pollen is lost and the ovules become

[4] KUSANO, S., Experimental studies on the embryonal development in an angiosperm. Jour. Coll. Agric. Tokyo **6**:7–120. *pls. 5–9. figs. 28.* 1915.

incapable of fertilization. Although the development of ovules and embryo sacs is promoted by the presence of pollen tubes, they are completed in unpollinated flowers unless nutritive conditions are too severe. In such flowers the egg apparatus may remain in healthy condition 8 or 9 days. In some cases it then degenerates; in other cases the ovule forms an embryoless seed, the number of these seeds in the fruit depending upon nutrition. Such embryoless seeds may develop from ovules with either the haploid or the diploid egg.

If the floral axis is separated from the tuber, scarcity of food material causes an imperfect development of ovarial and ovular tissue in pollinated flowers, but it does not interfere with the number of ovules going into seed formation nor with the development of the embryo. If pollinated flowers are cut from the floral axis and kept moist, fertilization occurs but the ovary does not grow. Some of the ovules develop into seeds with imperfect coats, while others degenerate after one or two embryonal divisions have occurred. The effects of reduced nutrition are here manifest. Of all the parts the embryo is the least liable to be retarded in development by poor nutritive conditions. It is evident that the embryo can develop without the accompanying development of the ovule or ovary tissue, and that the seed coat may likewise form without the development of the embryo or ovary wall. The growth of the latter, however, seems to be dependent upon the development of the ovules.

Self-pollination appears to be as effective as cross-pollination in *Gastrodia*. The pollinium will germinate within the cavity of the ovary and effect fertilization. Pollination with foreign (*Bletia*) pollen resulted in fruits and seeds of normal form and size, but the seeds were without embryos; no fertilization occurred. If both *Gastrodia* and *Bletia* pollen are placed on the same stigma the fertilizing activity of the *Gastrodia* pollen is greatly hindered.

With regard to parthenocarpy, the author recalls the distinction between vegetative (WINKLER) or autonomic (FITTING) parthenocarpy, in which embryoless fruits are formed without the agency of any external factor, and stimulative (WINKLER) or aitionomic (FITTING) parthenocarpy, in which the formation of embryoless fruit is induced by pollen or some other agent. Both types occur in *Gastrodia;* the aitionomic fruits are of normal size, while the autonomic ones are much smaller. The former appear to be well developed because the pollen or other agent stimulates nutritive activity; it seems that the size of the fruit may depend upon the intensity of the stimulus and also upon its duration. Parthenocarpic development of the ovary is dependent upon ovular development, the amount of seed apparently governing the size of the capsule.

Polyembryony occurs frequently in *Gastrodia*, and is correlated with delayed pollination. One embryo arises from the fertilized egg, and the other probably from a fertilized synergid.

Although diploid eggs occur frequently in *Gastrodia* their apogamous development was not observed in any case. It is interesting to note, however, that KUSANO saw several cases in which the nucleus of a haploid egg under-

went division. This is the first step in true parthenogenesis, but it is never accompanied by cell division and never leads to embryo formation. Other works on apogamy are cited, but the author believes the cytological facts regarding such matters are yet too few to warrant the formulation of a hypothesis on the evolution of parthenogenesis from amphimixis.

The value of contributions of this sort is obvious. The correlation of physiological conditions and morphological phenomena is clearly shown. This should lessen the morphologist's frequent neglect of physiology, and, on the other hand, should lead to a more careful checking up of experimental results, especially those in plant breeding, by morphological study.—L. W. SHARP.

Chromosomes and Mendelian inheritance.—STURTEVANT[5] presents a recapitulation with much new data bearing upon the "coupling" and "repulsion" of Mendelian genes in the fruit fly (*Drosophila ampelophila*), and ably discusses the bearing of these breeding results upon the chromosome interpretation of Mendelian phenomena. The large number of "cross-overs" (that is, changes from coupling to repulsion and vice versa between two given genes) and the relatively small number of chromosomes in the fruit fly, makes this organism very favorable material for such a study. Over 40 Mendelian characters of the fruit fly have been studied by MORGAN and his students, and these characters form four groups, so related to one another that all of the characters within one of these groups show "linkage" with one another; while those which have been sufficiently studied are independent of genes included in any one of the other groups. Each of these groups of characters is believed to be carried by a single pair of homologous chromosomes. On the basis of the relative number of cross-overs between different genes, considered two by two, the number of cross-overs which may be expected in any untried combination among the same series of "linked" genes may be readily calculated. Each gene is assumed to occupy a definite position or "locus" in the chromosome, and these loci are represented as forming a linear series whose distances from one another is measured by the relative frequency of cross-over. When cross-overs between two genes are rare, the two loci involved are assumed to be very near each other, and when cross-overs are frequent it is assumed that the two loci in question are correspondingly removed, though still lying in the same chromosome. No less than six of these loci have been established in a single chromosome, by a fairly adequate amount of data, and the correspondence between calculated distances and the observed numbers of cross-overs is convincing as to the fundamental value of this method of representation. Furthermore, the discrepancies between the observed and calculated results are so consistently in the same direction that they make possible another important

[5] STURTEVANT, A. H., The behavior of the chromosomes as studied through linkage. Zeitschr. Ind. Abstamm. Vererb. **13**:234–266. 1915.

generalization; namely that the occurrence of one cross-over in a chromosome lessens the likelihood that a second cross-over will take place in the same chromosome. This phenomenon the author describes as "interference." Following MORGAN, the author explains the phenomenon of crossing over as due to the twisting together of homologous chromosomes, and the failure to completely untwist when the chromosomes are separated—the "chiasmatype" of JANSSENS. Two cross-overs, or even three, may take place in the same chromosome when a series of loci sufficiently removed from one another are involved, but the frequency of such plural cross-overs is correspondingly low. While the percentage of cross-overs between any two "linked" characters was fairly constant in most of the material which has been studied by MORGAN and his students, the author points out that in certain strains there was a great deal of variation in the intensity of linkage. A part of this variability seems to be hereditary, but it is also suggested that some of the variation is probably due to conditions of food, etc. Most of the data regarding this variability are withheld for presentation and discussion in subsequent publications.

The author discusses the relation of chromosomes to Mendelian inheritance, and gives a list of 17 species of plants and animals in which clear cases of linkage have been described, and also a list of chromosome numbers which have been found in 25 species of plants and animals used in genetic experiments. He points out, as has been done by a number of geneticists, that each unit character is directly or indirectly due to the action of numerous Mendelian genes, and that each gene may and usually does affect a number of characters. The terminology used by the author, following that of MORGAN, is in one respect essentially the reverse of the one now most widely used, in that the symbols chosen to represent any Mendelian pair are based on the recessive instead of the dominant character; thus, instead of *Cc* for the factor for color, *Ww* is used, intending to suggest that in the absence of *W* a white individual results. This is just as usable a method of formulation as that now in general use, and has only the disadvantage that would be due to any such reversal of terminology. It has the strong pedagogical advantage that any dominant character is less likely to be misconstrued by the non-specialized reader, as the sole result of the single gene represented by the symbol.—G. H. SHULL.

A case of obligate symbiosis.—RAYNER[6] has discovered a very interesting case of obligate symbiosis between *Calluna vulgaris* and one of the mycorhiza. He has carried his investigations into careful experimental work, so that the details of the symbiosis in connection with the life history of *Calluna* have been discovered. It seems that infection by the fungus takes place shortly after germination, the source of the infection being the testa. This infection does not cease with the development of the mycorhiza in the roots, but affects

[6] RAYNER, M. C., Obligate symbiosis in *Calluna vulgaris*. Ann. Botany **29**:97–153. *pl. 6. figs. 4.* 1915.

all parts of the seedling, from whence it extends to all parts of the mature plant; that is, into the tissues of the stem, leaf, flower, and fruit. The ovary becoming infected, the mycelium enters the seed coats of the developing seeds, but the embryo and endosperm are free from infection. The fungus was isolated in pure cultures, and the seeds sterilized, so that a synthesis of the fungus of *Calluna* was accomplished. It was found that in case this specific fungus did not infect the growing seedling, it did not develop roots, and suffered complete inhibition of growth, remaining alive but rootless for several months. The fungus concerned is said to resemble the genus *Phoma*, and the author proposes that the species should be placed in a new subgenus, for which the name *Phyllophoma* is suggested.—J. M. C.

Development and distribution of Leguminosae.—ANDREWS[7] has brought together all the data dealing with the development and distribution of Leguminosae, and has reached certain conclusions of general interest. His thesis is that "the present distribution of plants and animals is the algebraic sum of the responses made by organisms to their changing environment during the whole of the known geological record, and the present adjustment of the activities involved has been obtained only after ages of development during various geographical changes." This is a problem, therefore, which involves the cooperation of geology, geography, and biology. ANDREWS finds that many uniform types of Leguminosae are widely diffused through the tropics, and that in extra-tropical countries these uniform tropical forms are represented by specialized types, which are mainly xerophytic. The details are fully presented, and it is thought that such study will throw light upon the nature of former land connections. For example, the author thinks that the Leguminosae show that New Zealand was separated from the tropics early in the differentiation of the family, while Australia was cut off at a date considerably later.—J. M. C.

Growth of Nereocystis.—Accurate data concerning the behavior of the large marine algae are much needed, the usual statements of the textbooks being vague and often misleading. This need promises to be supplied by the work of the Puget Sound Marine Station, whose first publication describes the growth of the blades of *Nereocystis Luetkeana*. Miss FALLIS[8] finds that this species grows as well when loosened from its foothold on the rocks, the holdfast serving only to fix the plant. Nor is the stipe, including the bulb, necessary for the growth of the blade, small pieces from which can grow independently. The growing region is not at the place of transition, between the blade and stipe, but its basal limit is at the beginning of the flattened part of the

[7] ANDREWS, E. C., The development and distribution of the natural order Leguminosae. Jour. Proc. Roy. Soc. N.W. Wales **48**:333–407. 1914.

[8] FALLIS, ANNIE L., Growth of the fronds of *Nereocystis Luetkeana*. Puget Sound Marine Station Publ. **1**:1–8. 1915.

blade, while its terminal limit is difficult to determine, because growth gradually decreases toward the tip of the blade.

A second paper, by Miss SHELDON,[9] deals with the growth of the stipe. It was found that the region of maximum growth in mature plants is 2–4 feet below the blade, the rate decreasing in both directions. In July the rate of growth was found to be about an inch a day.—J. M. C.

Ferns of the oriental tropics.—The richness of the fern vegetation of the tropics is being emphasized by the work of COPELAND.[10] In the papers cited, new species are described in the following genera: *Adiantum*, *Aglaomorpha* (a new subgenus *Holostachyum*, including two other species, being described), *Angiopteris*, *Asplenium*, *Athyrium* (6), *Balantium*, *Cyathea* (6), *Davallia*, *Dryopteris* (6), *Leptochilus*, *Loxogramme* (2), *Marattia*, *Microlepia*, *Oleandra*, *Ophioglossum*, *Polypodium* (8), *Prosaptia*, *Pteris*, *Tectaria* (4), *Trichomanes*, and *Vittaria*. The genera *Diplora* and *Triphlebia* were found to be invalid, because founded upon inconstant and "illusory" features, and should be included in *Phyllitis*, which comprises only three well defined species in the Malay-Polynesian region.—J. M. C.

Sphagnum bogs of Alaska.—RIGG[11] has noted the peculiarities of the flora of some Alaskan peat bogs and finds that while sphagnum occurs in many different habitats in Alaska, only where there is an absence of drainage do bogs accompany it. The peat in the bogs visited had a maximum depth of only 2.5 ft. Aside from the sphagnum, *Empetrum nigrum* is the most abundant and uniform in its occurrence, but *Ledum palustre*, *Kalmia glauca*, *Oxycoccus oxycoccus*, and *Drosea rotundifolia* are among other characteristic species. The bogs occur surrounded by treeless areas, by tundras, or by coniferous forests, and vary much in area.—GEO. D. FULLER.

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[9] SHELDON, SARAH M., Notes on the growth of the stipe of *Nereocystis Luetkeana*. *Ibid.* **1**:15–18. 1915.

[10] COPELAND, E. B., The ferns of the Batu Lawi Expedition. Appendix III. Roy. Agric. Soc. (Straits Branch). no. 63. 71–72. 1912.

———, Some ferns of northeastern Mindanao. Leaflets Philipp. Bot. **5**:1675–1684. 1913.

———, Notes on some Javan ferns. Philipp. Jour. Sci. **8**:139–145. *pls. 2–4*. 1913.

———, On *Phyllitis* in Malaya and the supposed genera *Diplora* and *Triphlebia*. *Ibid.* **8**:147–155. *pls. 5–7*. 1913.

———, New Papuan ferns. *Ibid.* **9**:1–9. 1914.

———, New Sumatran ferns. *Ibid.* **9**:227–233. 1914.

[11] RIGG, G. B., Notes on the flora of some Alaskan sphagnum bogs. Plant World **17**:176–183. 1914.